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UNITED STATES DEPARTMENT OF THE INTERIOR, DOUGLAS McKAY, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

FLUCTUATIONS IN THE FISHERIES OF STATE OF MICHIGAN WATERS OF GREEN BAY

By RALPH HILE, GEORGE F. LUNGER
and HOWARD J. BUETTNER

March 3, 1849

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FLUCTUATIONS IN THE FISHERIES OF STATE OF MICHIGAN WATERS OF GREEN BAY

By **Ralph Hile**, *Fishery Research Biologist*, and **George F. Lunger** and **Howard J. Buettner**, *Statisticians*

Green Bay,[1] traditionally a major center of production, has assumed in recent years a position of overwhelming dominance in the commercial fisheries of the State of Michigan waters of Lake Michigan. Within the 4-year period 1945–48 the commercial take in State of Michigan waters of Green Bay increased from 3,317,000 pounds in 1945 to 7,909,000 pounds in 1948, and it was 7,782,000 pounds in 1949. At the same time the percentage contribution of Green Bay to the State total for Lake Michigan rose each year, increasing from 36.5 in 1945 to 65.4 in 1949.

The tremendous upswing in commercial production in Green Bay can be attributed to the abnormally high abundance of three important species—the lake whitefish (*Coregonus clupeaformis*), the lake herring or shallowwater cisco (*Coregonus* [=*Leucichthys*] *artedii*), and the walleye or yellow pikeperch (*Stizostedion v. vitreum*)—and to a marked rise in fishing intensity. The increase in the abundance of fish was to a great extent responsible for the rise in fishing pressure. Not only were local fishermen stimulated to greater efforts, but commercial operators from many other localities moved into Green Bay to participate in the good fishing. Most numerous, perhaps, among the newcomers were fishermen from Lake Huron who were literally driven from home by the declining productivity of their own fishing grounds. Fishermen from Wisconsin, also, purchased nonresident licenses for fishing in State of Michigan waters.

The heightened production in Green Bay has not proved an unmitigated blessing. The influx of fishermen from other localities has resulted in severe congestion of the fishing grounds. Frictions have arisen and unpleasant incidents have occurred. These difficulties are likely to be multiplied at such time as the abundance of fish approaches a more nearly normal level, for the available stocks then may prove inadequate to support profitable operations by all the fishermen now concentrated in the area.

Still another problem is offered by the greatly heightened interest of sportsmen and resort owners in the walleye. They have found the recent high abundance of walleyes greatly to their liking and wish to see it perpetuated. To that end some are willing to press for stringent limitations on commercial operations—restrictions on gear, closure of grounds, even placing the walleye on the game-fish list.

Thus we have all the elements needed to create a difficult and turbulent situation in northern Green Bay in the years ahead. The decline in abundance of fish that seems almost certain to come will prove distressing to all groups. Should these groups resort to pressures to obtain changes of regulations—either liberalized or restrictive—without first making certain that the changes are sound, the welfare of the fisheries could be gravely endangered. The best interests of the various groups are not incompatible, but their views frequently are. If the several groups are to be brought together, it will come about through a better understanding and appreciation of facts relating to the fisheries.

It is to be regretted that the available facts on the fisheries of Green Bay are few. Past studies of the biology of fishes in the area, though instructive, have been scattered. Opportunities have been lacking for the continuity of research so essential to an appreciation of the tremendous changes that take place within populations. Until better understanding of these changes is developed we shall continue at a severe disadvantage in attempting to prescribe for the welfare of the fisheries.

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[1] The designation, Green Bay, as employed in this paper refers to State of Michigan waters only.

Despite the inadequacy of the biological background, we have useful information on the Green Bay fisheries. Particularly valuable are statistical data for the 21-year period 1929–49 which permit accurate description of the changes in production and good estimates of fluctuations in fishing pressure and in abundance of the principal species. True, the causes of the changes in abundance continue to be unknown; nevertheless, sounder thinking is promoted when we are in position to describe changes quantitatively. Reasonably dependable norms can be established and exceptional situations evaluated more effectively.

This paper on the Green Bay fisheries is documentary and its discussions are generally descriptive rather than analytical. Its primary purpose is to make the more significant statistical data available in concise form to investigators, conservation officials, sportsmen, industry, and others interested in the future of the fisheries. It is hoped that this review of past changes in the fishery will make possible a better understanding of the situation as it exists now and of the changes that may come about within the next few years.

Portions of the statistical data given in this paper were included in earlier publications by Hile (1937) on the artificial propagation of the walleye in Lakes Huron and Michigan; by Van Oosten, Hile, and Jobes (1946) on the whitefish fishery of Lakes Huron and Michigan; by Van Oosten (1947) on the smelt (*Osmerus mordax*) mortality of 1942–43 in the same lakes; by Hile (1950) on the recent phenomenal rise in the abundance of walleyes in Green Bay; and by Hile, Eschmeyer, and Lunger (1951a) on the decline of the fishery for lake trout (*Salvelinus namaycush*) in Lake Michigan. These earlier papers, however, dealt with special problems and undertook no review of the Green Bay fishery as a whole.

The authors wish to express appreciation to Dr. James W. Moffett for his helpful criticisms of the original manuscript; to Elmer Higgins who offered many useful suggestions on the section concerning the problem of economically sound regulations; and to Dr. Reeve M. Bailey, Curator of Fishes, Museum of Zoology, University of Michigan, for his valuable advice on the nomenclature of Green Bay fishes.

SOURCES OF DATA AND METHODS OF ANALYSIS

Data on production in 1885 were taken from Smith and Snell (1891) and those for 1891–1908 were compiled (with WPA assistance) from handwritten records turned over to the U. S. Fish and Wildlife Service by the Michigan Department of Conservation.

Statistics on production and estimates of the fluctuations in abundance of the principal species and in intensity of the fishery in 1929–49 have been based on reports of commercial fishing submitted each month to the Michigan Department of Conservation by all fishermen licensed to operate in the Great Lakes waters of the State, and subsequently released to the Fish and Wildlife Service for detailed analysis.

The methods employed in statistical analysis of the commercial fisheries of the Great Lakes have been described in earlier publications by Hile (1937), Hile and Jobes (1941), and Van Oosten, Hile, and Jobes (1946). Two points only need be stressed here. First, estimates of abundance of a particular species are derived from records of the actual catch in pounds per standard unit of fishing effort (lift of 10,000 linear feet of gill net; lift of 1 pound, trap, or fyke net; . . .). Second, estimates of the intensity of the fishery for a particular species are based only on gear lifted on days when some quantity of the species was captured by the fisherman submitting the report.

COMMERCIAL PRODUCTION IN GREEN BAY

PRODUCTION IN 1885

The earliest published review containing usable statistics on the commercial production of fish in Green Bay was that made for 1885 by Smith and Snell (1891). The catch statistics for Big Bay de Noc (including grounds in the Summer Islands area), Escanaba and vicinity, and Menominee County were combined to obtain the data of table 1.[2] (See fig. 1 for chart of area.)

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[2] The figures given in table 1 represent our best judgment in the resolution of certain discrepancies in the data of Smith and Snell. The text relating to the Big Bay de Noc area mentioned 812 100-pound packages of salted walleyes but included no reference to salted lake trout. The statistics for the same area in the general tables for Lake Michigan, however, showed 81,200 pounds of salted lake trout and 2,000 pounds of salted "pike and pickerel." In our summarization we followed the table. Again, the text concerning the fisheries for Escanaba and vicinity mentioned

TABLE 1.—*Commercial production of fish, by species, in Green Bay, 1885*

[In thousands of pounds; data adapted from Smith and Snell (1891)]

Species	Production	Percentage of total
Lake trout	404	16.5
Whitefish [1]	758	31.0
Lake herring	972	39.7
Walleye [2]	91	3.7
Suckers	48	1.9
Sturgeon	131	5.3
Black bass	4	.2
Miscellaneous [3]	41	1.7
Total	2,449	------------

[1] Includes round whitefish (*Prosopium cylindraceum*) and blackfins (*Coregonus nigripinnis*). The catch of these species doubtless was small; statements by Smith and Snell concerning quantities of blackfins captured in the vicinity of Escanaba must be viewed with skepticism.

[2] Believed to have been mostly walleyes. Smith and Snell confused the terms "walleyed pike," "pike," "pickerel," and "doré" in their text.

[3] Fish mentioned specifically as having part or all of their catch included under "Miscellaneous" were black bass (*Micropterus* spp.), suckers (*Catostomus* spp. and *Moxostoma* spp.), yellow perch (*Perca flavescens*), and bullheads (*Ameiurus* spp.).

Lake herring (39.7 percent of the total of 2,449,000 pounds) and whitefish (31.0 percent) predominated in the 1885 fishery. Lake trout (16.5 percent) also was important, but among the remaining species only the lake sturgeon (*Acipenser fulvescens*) contributed as much as 5 percent of the total.

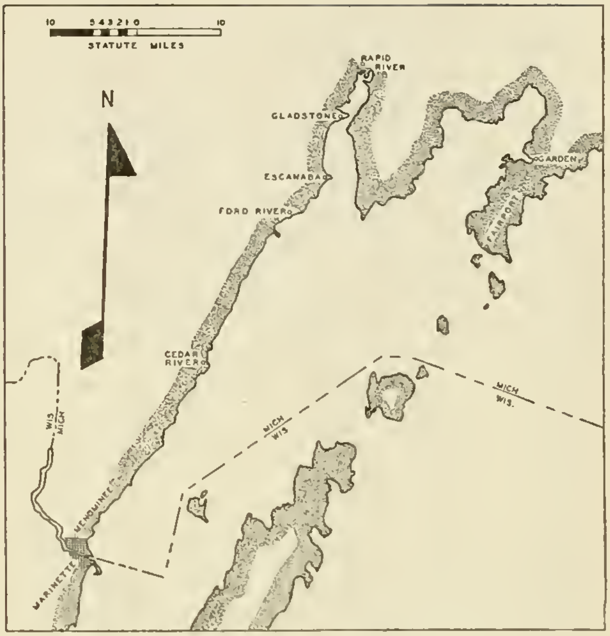

FIGURE 1.—Chart of northern Green Bay.

PRODUCTION IN 1891–1908

Outstanding features of the statistics for this 18-year period (tables 2 and 3; figs. 2 to 8) were the pronounced if irregular upward trend of production and the strong dominance of lake herring in the catch. Of significance also was the increased relative importance of yellow perch and suckers in the latter part of the period.

TABLE 2.—*Production in the commercial fisheries of Green Bay, by species, 1891–1908*

[In thousands of pounds]

Year	Lake trout	Whitefish	Lake herring	Walleye	Yellow perch	Suckers	Lake sturgeon	Miscellaneous [1]	Total catch
1891	171	78	1,515	121	------------	8	47	154	2,093
1892	35	149	1,645	214	11	19	38	129	2,241
1893	174	123	2,898	163	32	100	25	252	3,767
1894	142	89	1,956	186	41	16	30	50	2,510
1895	109	72	3,413	301	37	99	24	60	4,115
1896	119	89	3,890	300	39	38	31	52	4,558
1897	176	84	6,205	286	114	182	19	72	7,138
1898	161	85	7,164	267	78	179	24	80	8,037
1899	127	112	9,606	209	78	358	22	86	10,598
1900	90	83	5,781	183	62	387	17	157	6,762
1901	168	98	5,198	146	83	369	12	175	6,249
1902	307	140	7,169	183	131	545	14	166	8,656
1903	380	228	6,153	258	312	776	19	103	8,229
1904	363	283	8,569	120	342	582	16	53	10,327
1905	382	348	5,300	106	499	693	12	58	7,399
1906	332	292	7,526	202	355	891	12	45	9,655
1907	299	292	9,300	185	247	1,124	11	36	11,494
1908	300	222	11,850	121	367	798	17	32	13,708
Mean, 1891–1908	213	159	5,841	197	157	398	22	98	7,085
Percentage	3.0	2.3	82.4	2.8	2.2	5.6	0.3	1.4	100

[1] Includes small production of black bass, sauger (*Stizostedion canadense*), and catfish (presumably *Ictalurus punctatus*) in addition to catches not identified.

520,294 pounds of smoked fish—a poundage exactly equal to the combined totals of fresh and salt fish listed in the general tables. The tables recorded no smoked fish for the Escanaba region. Here, again, we followed the tables.

TABLE 3.—*Percentage composition of the catch, by species, in the commercial fisheries of Green Bay, 1891–1908*

Year	Lake trout	Whitefish	Lake herring	Walleye	Yellow perch	Suckers	Lake sturgeon	Miscellaneous
1891	8.2	3.7	72.4	5.8	-------	0.4	2.2	7.3
1892	1.6	6.6	73.5	9.6	0.5	.8	1.7	5.7
1893	4.6	3.3	76.9	4.3	.8	2.7	.7	6.7
1894	5.6	3.6	78.0	7.4	1.6	.6	1.2	2.0
1895	2.6	1.8	82.9	7.3	.9	2.4	.6	1.5
1896	2.6	1.9	85.3	6.6	.9	.8	.7	1.2
1897	2.5	1.2	86.9	4.0	1.6	2.5	.3	1.0
1898	2.0	1.1	89.1	3.3	1.0	2.2	.3	1.0
1899	1.2	1.1	90.6	2.0	.7	3.4	.2	.8
1900	1.3	1.3	85.5	2.7	.9	5.7	.3	2.3
1901	2.7	1.6	83.2	2.3	1.3	5.9	.2	2.8
1902	3.6	1.6	82.8	2.1	1.5	6.3	.2	1.9
1903	4.6	2.8	74.8	3.1	3.8	9.4	.2	1.3
1904	3.5	2.7	83.0	1.2	3.3	5.6	.2	.5
1905	5.2	4.7	71.6	1.4	6.7	9.4	.2	.8
1906	3.4	3.0	78.0	2.1	3.7	9.2	.1	.5
1907	2.6	2.5	80.9	1.6	2.2	9.8	.1	.3
1908	2.2	1.6	86.5	.9	2.7	5.8	.1	.2
Mean	3.3	2.6	81.2	3.8	1.9	4.6	.5	2.1

The total catches in 1891 (a little more than 2 million pounds) and 1892 (about 2¼ million pounds) were below the 1885 level. The take rose to about 3¾ million pounds in 1893, dropped to 2½ million pounds in 1894, and then entered on a 5-year period of consistent increase which culminated in a catch of 10½ million pounds in 1899. A 4-year period, 1900–1903, of somewhat lower yield—approximately within the range of 6¼ to 8½ million pounds—was followed by a second peak of more than 10¼ million pounds in 1904. Again the take dropped sharply (nearly to 7¼ million pounds) in the year after the peak. From the relatively low 1905 value the yield increased rapidly to about 9½ million pounds in 1906, to 11½ million pounds in 1907, and to 13¾ million pounds in 1908. The last figure represents not only the maximum for the 18-year period but also the highest recorded yield for the State of Michigan waters of Green Bay.

Comparison of the statistics on the total catch with those for the lake herring reveals that the fluctuations in the take of this species were in large measure responsible for the trends of total production. Lake herring made up 82.4 percent of the 1891–1908 catch (table 2) and did not contribute less than 71.6 percent (the figure for 1905—see table 3) in any single year. The percentage was consistently above 85 in the 5 years 1896–1900 and reached 90.6 in 1899. The output of lake herring increased from the relatively low figure of 1½ million pounds in 1891 to more than 2¾ million in 1893, dropped to less than 2 million pounds in 1894, and then increased each year until a peak of more than 9½ million pounds was reached in 1899. The take varied irregularly during the next several years. Toward the end of the 18-year interval a second period of consistent increase carried the output from about 5¼ million pounds in 1905 to more than 11¾ million pounds in 1908.

Most of the other species that contributed more than 2 percent to the total 1891–1908 yield (yellow perch formed 2.2 percent of the 1891–1908 total, table 2, but had a mean percentage of only 1.9, table 3) exhibited the same upward trend of production that characterized the lake herring. The catch of lake trout, for example, did not exceed 176,000 pounds (the take in 1897) in the years 1891–1901, but was 300,000 pounds or more in 6 of the 7 years 1902–08. Similarly, in 1891–1902, the take of whitefish was greater than 100,000 pounds in only 4 years and was never as high as 150,000 pounds, but exceeded 200,000 pounds every year after 1902.

Discussion of the increase in the output of yellow perch and suckers is handicapped by the circumstance that part of the catch of both probably was included under Miscellaneous, especially during the earlier years of the 1891–1908 period. Despite this difficulty it is valid to state that the take of yellow perch and suckers did increase greatly toward the end of the period. This conclusion would hold even if we were to assume that perch and suckers made up practically all of the miscellaneous catch in the earlier years and little or none in the later ones. The increase in the production of suckers was sufficient to place that species second only to lake herring in every year after 1898 and in the 18-year average. The contribution of suckers to the annual totals exceeded 5 percent every year after 1899 and was over 9 percent in 4 years. The increase in the production of yellow perch carried that species from a position of insignificance to the point where it held third place in 1905, 1906, and 1908 and accounted for as much as 6.7 percent of the total catch (in 1905).

The walleye provides an exception to the trends just described for the other principal species. Most of the larger catches were in the earlier part of the 18-year period, with the four best years in 1895–98. The take was more than 200,000 pounds in 6 of the 9 years 1891–99, but in only 2 of the 9 years 1900–1908. The downward trend was even more pronounced in the percentage contribution of walleyes to the annual totals. This percentage was 4 or greater in every year before 1898 and was as high as 9.6 (in 1892). During the last 11 years of the period, walleyes made up more than 3 percent of the annual yield only twice and accounted for less than 2 percent in 4 years.

The production of sturgeon, a species once abundant in the Green Bay area (*cf.* Milner 1874, Smith and Snell 1891), already had fallen to a low level by 1891. The decline continued irregularly during the 1891–1908 period.

Too much should not be made of a comparison of production in 1891–1908 with that in 1885 since we cannot be certain that conditions in the single earlier year were representative of the middle 1880's. It does appear, however, that the species composition of the catch changed markedly from 1885 to the early 1890's even though the actual total yield did not rise to a point consistently above the 1885 level until 1895. It is true that the lake herring was the principal fish taken in 1885 as it was in 1891–1908; but the percentage contribution to the total was only 39.7 in 1885 as compared with 82.4 (range, 71.6 to 90.6) in the later years. Whitefish, on the contrary, fell from 31.0 percent in 1885 to 2.3 percent (range, 1.1 to 6.6) in 1891–1908. The percentage for lake trout also declined markedly from 16.5 to 3.0 (range, 1.2 to 8.2).

PRODUCTION IN 1929–49

Data on the average take and on the percentage contribution of the leading species to the total yield have been given in tables 4 and 5 for the years 1929–43 and 1929–49. The former is the "period of reference" established for the description of fluctuations in the modern fishery of State of Michigan waters of the Great Lakes. The large discrepancies between certain figures for 1929–43 and 1929–49 suggest that in some areas an average or "normal" based on a period even as long as 15 years may have its limitations. In Green Bay the addition of only 6 years' data to those for 15 years raised the averages for the production of whitefish, lake herring, and walleyes by 297,000, 356,000, and 82,000 pounds, respectively. The corresponding percentage increases of 1929–49 over 1929–43 means for these species were: Whitefish, 71; lake herring, 50; walleyes, 161. For the remaining four principal species[3] the 1929–49 means were lower by 20,000 pounds (lake trout) to 108,000 pounds (smelt). The percentage decreases ranged from 5 for the suckers to 15 for the smelt. The average catch for all species in 1929–49 (3,582,000 pounds) was 544,000 pounds, or 18 percent greater than that for 1929–43 (3,038,000 pounds).

Of the two intervals, 1929–43 and 1929–49, the former probably represents the better reference period for the modern fishery since the high levels that have characterized the output of whitefish, lake herring, and walleyes in recent years can hardly be expected to persist indefinitely.

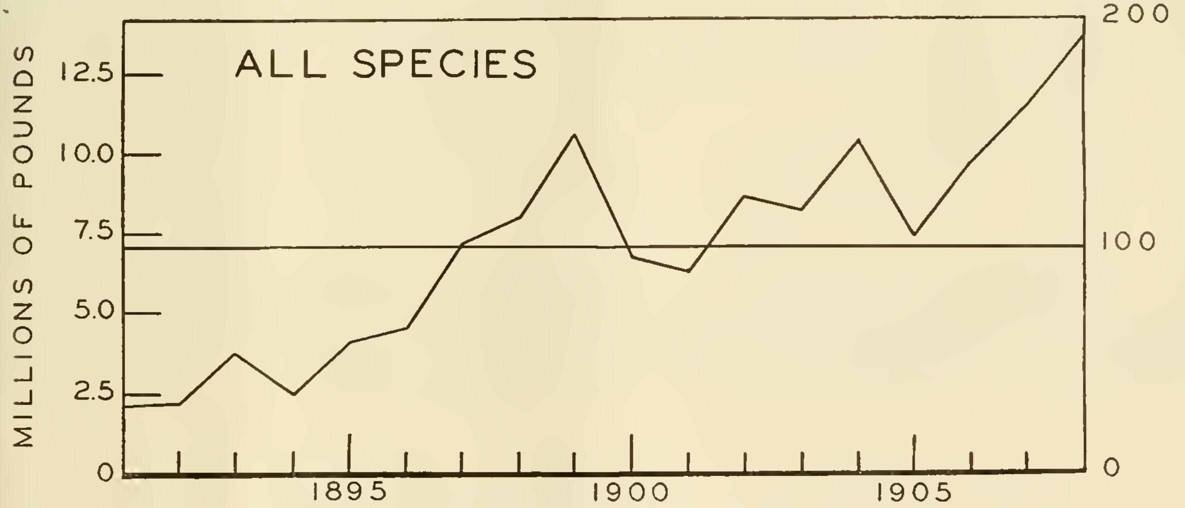

FIGURE 2.—All species: Commercial production in State of Michigan waters of Green Bay, 1891–1908, in millions of pounds and as percentages of the 18-year mean.

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[3] For purposes of discussion in this paper, white and redhorse suckers (*Catostomus commersoni* and *Moxostoma* spp.) are treated as a single species. Actually, the white sucker predominates strongly in this combined catch.

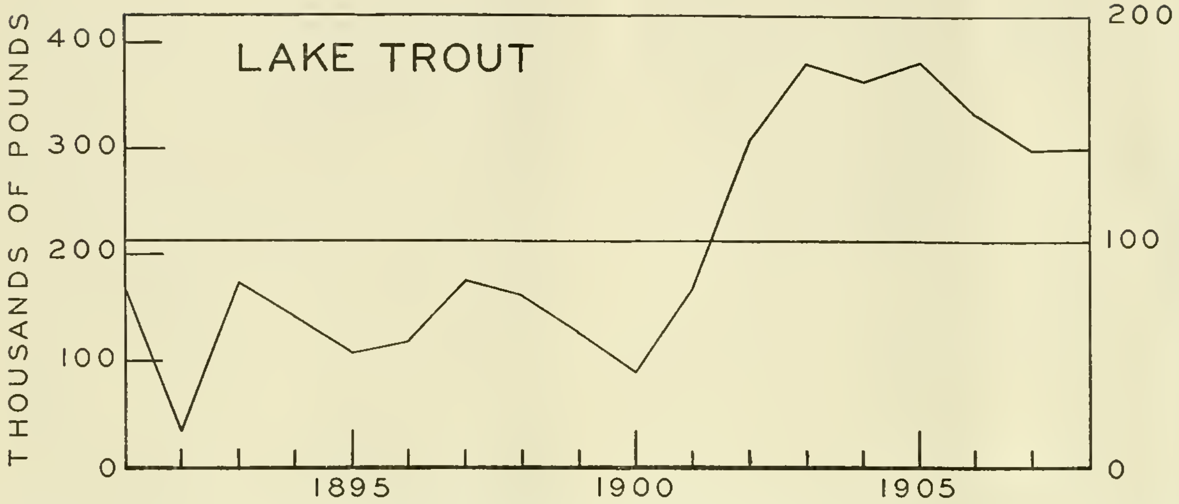

FIGURE 3.—Lake trout: Commercial production in State of Michigan waters of Green Bay, 1891–1908, in thousands of pounds and as percentages of the 18-year mean.

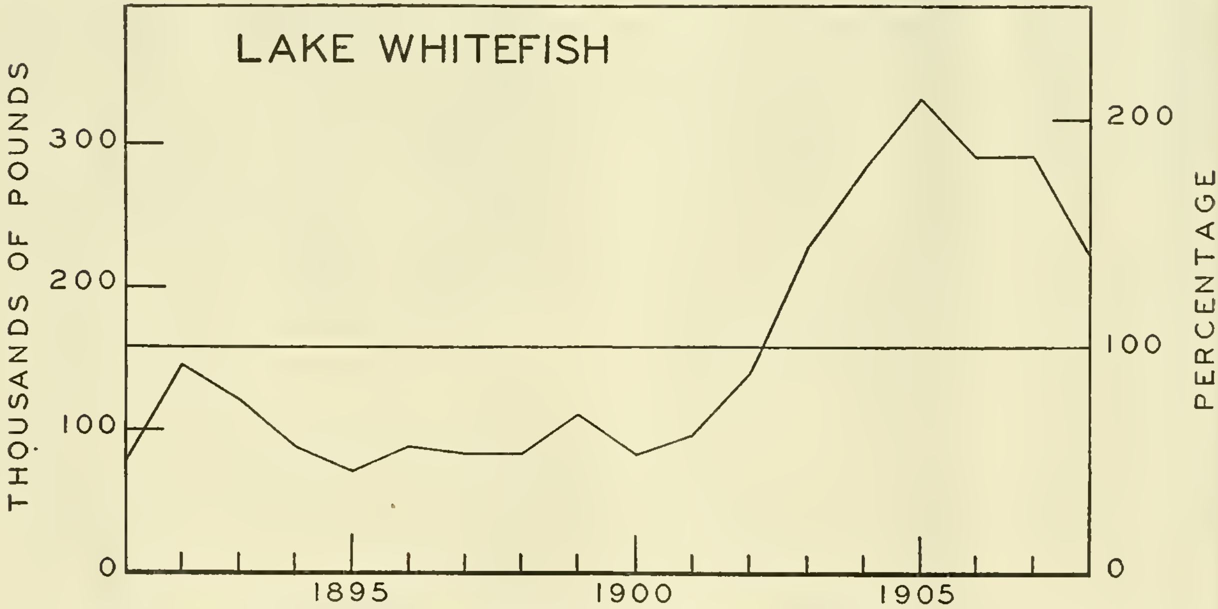

FIGURE 4.—Lake whitefish: Commercial production in State of Michigan waters of Green Bay, 1891–1908, in thousands of pounds and as percentages of the 18-year mean.

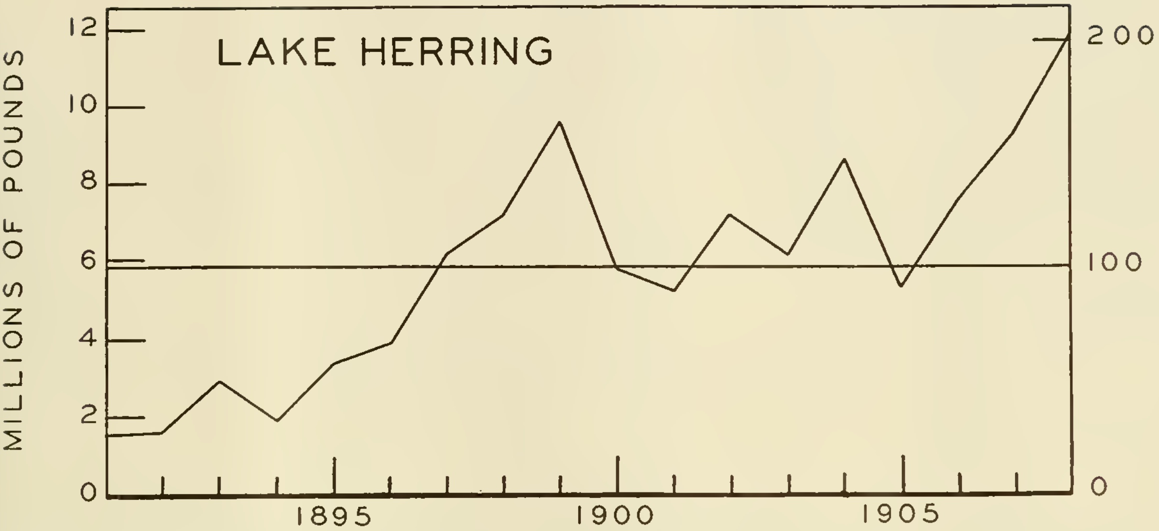

FIGURE 5.—Lake herring: Commercial production in State of Michigan waters of Green Bay, 1891–1908, in millions of pounds and as percentages of the 18-year mean.

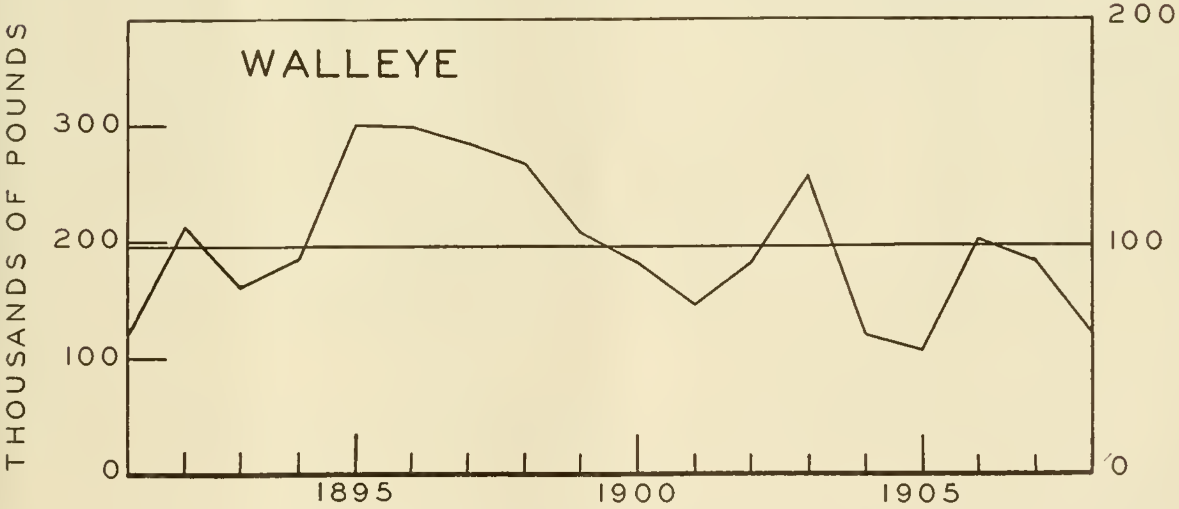

FIGURE 6.—Walleye: Commercial production in State of Michigan waters of Green Bay, 1891–1908, in thousands of pounds and as percentages of the 18-year mean.

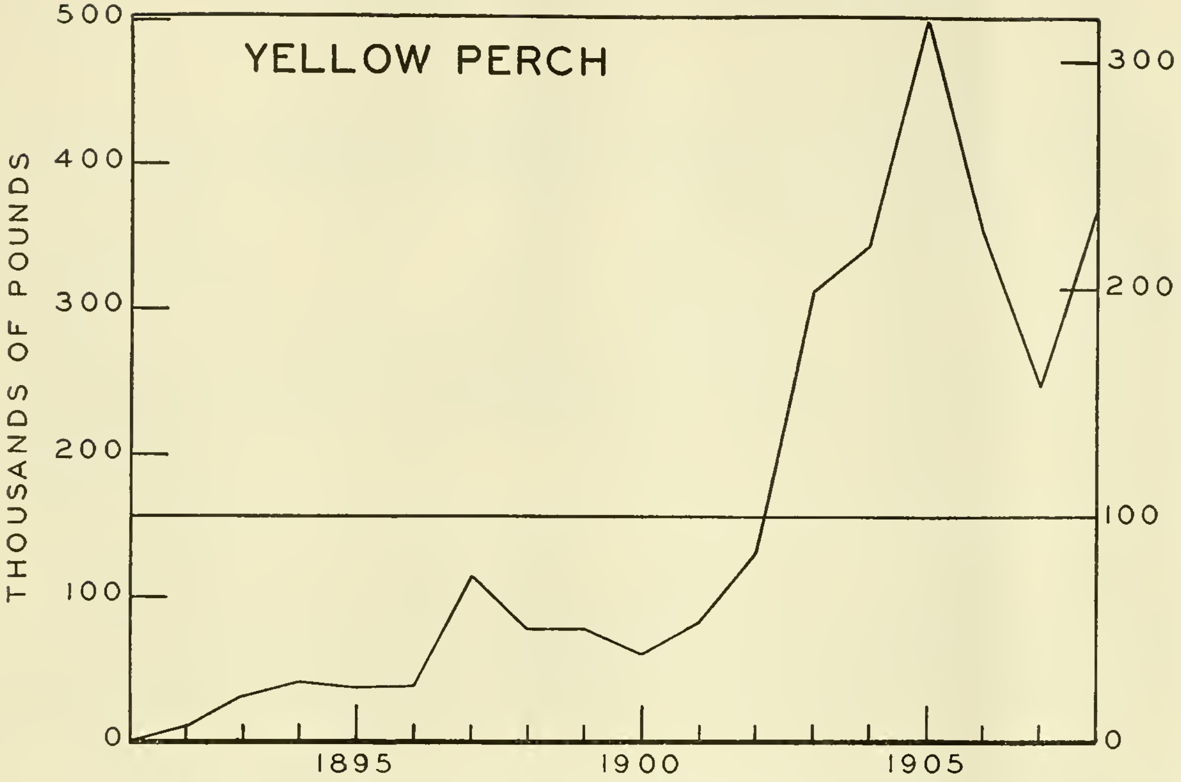

FIGURE 7.—Yellow perch: Commercial production in State of Michigan waters of Green Bay, 1891–1908, in thousands of pounds and as percentages of the 18-year mean.

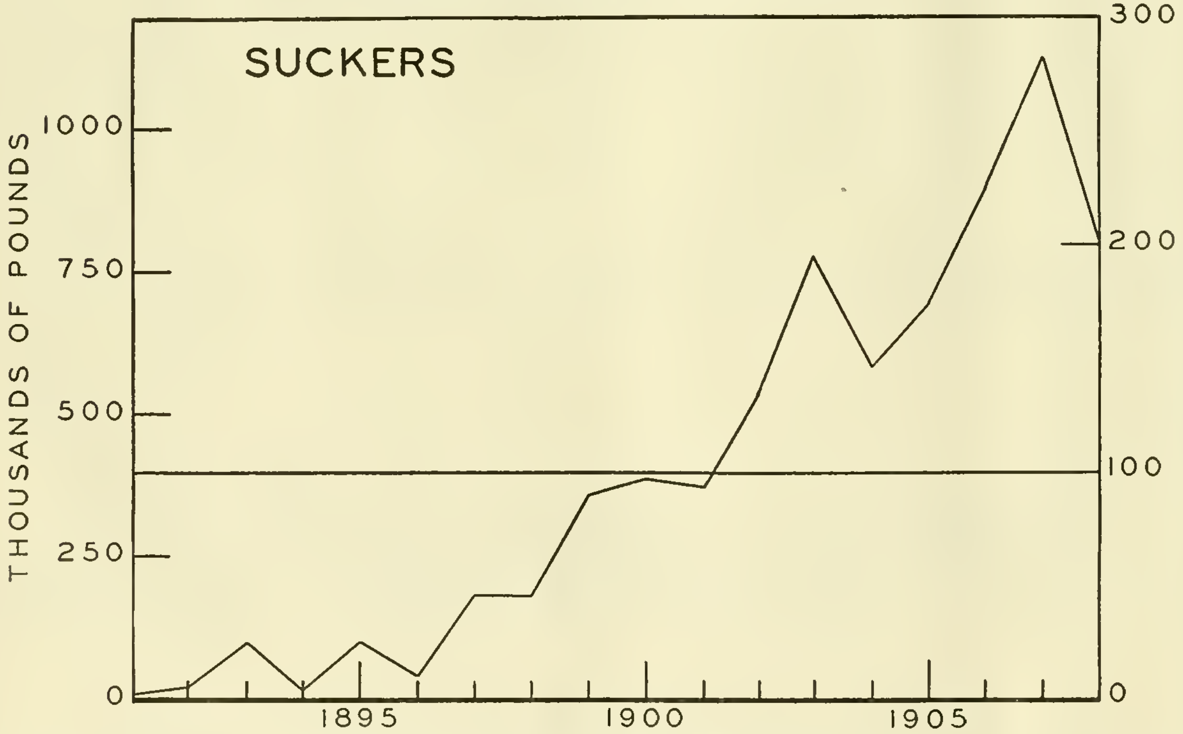

FIGURE 8.—Suckers (all species): Commercial production in State of Michigan waters of Green Bay, 1891–1908, in thousands of pounds and as percentages of the 18-year mean.

TABLE 4.—*Production in the commercial fisheries of Green Bay, by species, 1929–49*

[In thousands of pounds]

Year	Lake trout	Whitefish	Lake herring	Walleye	Yellow perch	White and redhorse suckers	Smelt	Others [1]	Total catch
1929	182	1,140	396	27	95	393	-------	86	2,319
1930	203	1,076	484	27	129	566	-------	163	2,648
1931	220	1,195	521	41	111	714	(2)	121	2,924
1932	194	910	170	85	130	858	23	119	2,489
1933	134	238	160	108	129	588	9	51	1,418
1934	72	263	16	108	172	763	17	73	2,384
1935	77	175	1,054	57	156	1,181	45	52	2,797
1936	158	90	1,271	74	142	982	114	56	2,888
1937	236	105	1,834	59	261	1,015	186	39	3,736
1938	248	354	1,552	38	361	718	672	61	4,004
1939	157	238	697	30	256	635	607	82	2,703
1940	83	123	668	28	170	719	2,392	26	4,209
1941	75	116	297	26	191	591	2,976	48	4,319
1942	56	93	285	16	203	665	2,212	44	3,574
1943	91	141	402	36	125	611	1,723	22	3,153
Mean, 1929–43	146	417	714	51	175	733	732	70	3,038
Percentage	4.8	13.7	23.5	1.7	5.8	24.1	24.1	2.3	-------
1944	47	232	419	43	49	564	(2)	25	1,379
1945	29	234	2,193	21	151	593	43	54	3,317
1946	11	514	2,367	72	116	505	66	41	3,692
1947	46	2,427	1,881	262	70	499	336	49	5,570
1948	178	3,066	2,668	572	66	634	626	99	7,909
1949	149	2,263	2,230	1,063	65	878	1,050	84	7,782
Mean, 1929–49	129	714	1,070	133	150	699	624	66	3,582
Percentage	3.5	19.9	29.9	3.7	4.2	19.5	17.4	1.9	-------

[1] Includes chubs, or ciscoes (*Coregonus* spp.), carp (*Cyprinus carpio*), round whitefish, burbot (*Lota lota*), bullheads, catfish, northern pike (*Esox lucius*), saugers, longnose suckers (*Catostomus catostomus*), sheepshead, or freshwater drum (*Aplodinotus grunniens*), white bass (*Morone chrysops*), rock bass (*Ambloplites rupestris*), bowfin (*Amia calva*), and garfish (probably *Lepisosteus osseus*).

[2] Less than 500 pounds.

TABLE 5.—*Percentage composition of the catch in the commercial fisheries of Green Bay, by species, 1929–49*

Year	Lake trout	White-fish	Lake herring	Walleye	Yellow perch	White and redhorse suckers	Smelt	Others
1929	7.8	49.2	17.1	1.2	4.1	16.9	-------	3.7
1930	7.7	40.6	18.3	1.0	4.9	21.4	-------	6.1
1931	7.5	40.9	17.8	1.4	3.8	24.4	0.0	4.2
1932	7.8	36.6	6.8	3.4	6.2	34.5	.9	4.8
1933	9.5	16.8	11.3	7.6	9.1	41.5	.6	3.6
1934	3.0	11.1	38.4	4.5	7.2	32.0	.7	3.1
1935	2.7	6.3	37.7	2.0	5.6	42.2	1.6	1.9
1936	5.5	3.1	44.0	2.6	4.9	34.0	4.0	1.9
1937	6.3	2.8	49.1	1.6	7.0	27.2	5.0	1.0
1938	6.2	8.8	38.8	1.0	9.0	17.9	16.8	1.5
1939	5.8	8.8	25.8	1.1	9.5	23.5	22.5	3.0
1940	2.0	2.9	15.9	.7	4.0	17.1	56.8	.6
1941	1.7	2.7	6.9	.6	4.4	13.7	68.9	1.1
1942	1.6	2.6	8.0	.4	5.7	18.6	61.9	1.2
1943	2.9	4.5	12.8	1.1	4.0	19.4	54.6	.7
Mean, 1929–43	5.2	15.8	23.3	2.0	5.9	25.6	19.6	2.6
1944	3.4	16.8	30.4	3.1	3.6	40.9	0.0	1.8
1945	.9	7.1	66.1	.6	4.5	17.9	1.3	1.6
1946	.3	13.9	64.1	2.0	3.1	13.7	1.8	1.1
1947	.8	43.6	33.8	4.7	1.2	9.0	6.0	.9
1948	2.3	38.8	33.7	7.2	.8	8.0	7.9	1.3
1949	1.9	29.1	28.6	13.7	.8	11.3	13.5	1.1
Mean, 1929–49	4.2	18.4	28.8	2.9	4.9	23.1	15.5	2.2

Catch records for the principal species in the individual years reveal a wide range of fluctuation in the take of all species and a strong tendency toward cyclic fluctuations in some. The trends of production for the different kinds and for the total catch are summarized briefly in the paragraphs that follow.

Lake trout: After increasing from 182,000 pounds in 1929 to 220,000 pounds in 1931, the take declined to a low of 72,000 pounds in 1934, rose to a second peak of 248,000 pounds in 1938, declined again (except for an irregularity in 1943) to a minimum of 11,000 pounds in 1946, jumped to 178,000 pounds in 1948, and dropped to 149,000 pounds in 1949.[4] (See fig. 9.)

Whitefish: Production exceeded a million pounds in each of the 3 years 1929–31, but from the high figure of 1,195,000 pounds in 1931 decreased (with an irregularity in 1934) to the 21-year minimum of 90,000 pounds in 1936 (fig. 10). A recovery to the relatively low peak of 354,000 pounds in 1938 was followed by another decline to 93,000 pounds in 1942. Successive increases in each of the next 6 years carried the take to the all-time recorded high of 3,066,000 pounds in 1948. The catch dropped to 2,263,000 pounds in 1949.

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[4] See Hile, Eschmeyer, and Lunger (1951a) for a discussion of the cause of the sharp recovery in the production of lake trout in 1948 and 1949.

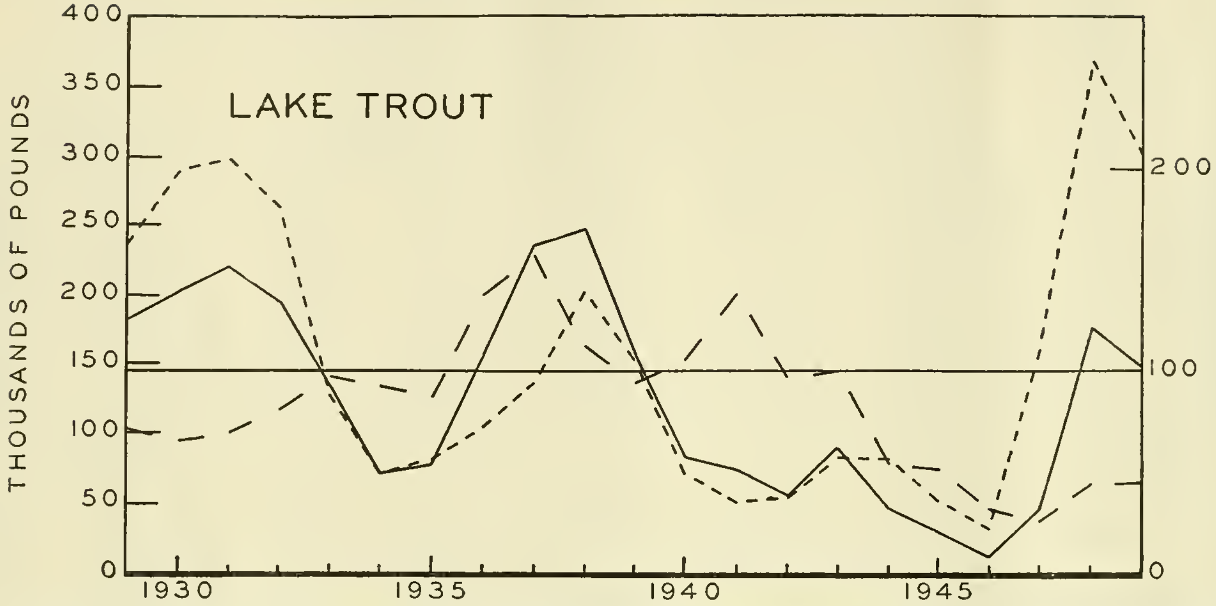

Figure 9.—Lake trout: Production (solid line), abundance (long dashes), and intensity of the fishery (short dashes) in State of Michigan waters of Green Bay, 1929–49, as percentages of the 1929–43 mean. Production is also given in pounds on scale at the left.

Lake herring: From a level of 396,000 pounds in 1929 the yield rose to 521,000 pounds in 1931, dropped to the 21-year minimum of 160,000 pounds in 1933, and then increased to 1,834,000 pounds in 1937 (fig. 11). A second decline, to a low of 285,000 pounds in 1942, was followed by yet another upward trend (interrupted by a decrease in 1947) which culminated in an output of 2,668,000 pounds, the 21-year maximum, in 1948. The 1949 yield was 2,230,000 pounds.

Walleye: The take rose from 27,000 pounds in 1929 and 1930 to 108,000 pounds in 1933 and 1934, and then declined irregularly to the minimum of 16,000 pounds in 1942 (fig. 12). Production continued to be relatively low during the next 3 years, but 1946 saw the start of an upswing that led to a record yield of 1,063,000 pounds in 1949.

Yellow perch: Production statistics for perch exhibit little indication of the cyclic fluctuations that characterized the lake trout, whitefish, lake herring, and to some extent, the walleye (fig. 13). Except for the high production of 1937–39 (catch more than 250,000 pounds in all 3 years and 361,000 pounds in 1938) and a tendency toward small yields in recent years (output below 100,000 pounds in 4 of the last 6 years and only 49,000 pounds in 1944) the fluctuations in the take of yellow perch can be described as erratic.

White and redhorse suckers: The catch of suckers, much like that of perch, varied erratically. (See fig. 14.) The principal features aside from this irregular fluctuation were the rise from the low catch of 393,000 pounds in 1929 to 714,000 pounds (near the mean level for 1929–43 and 1929–49) in 1931 and the high output in 1935–37 when the take was approximately a million pounds in three consecutive years.

Smelt: This introduced species (see Van Oosten 1937, for an account of its introduction and spread in the Great Lakes) first entered the commercial fishery in 1931 (less than 500 pounds caught). The take did not exceed 100,000 pounds until 1936 or 500,000 pounds until 1938 but large increases in 1940 and 1941 carried the output to nearly 3 million pounds in the latter year. From this 1941 peak the catch dropped to less than 500 pounds in 1944. The declines in 1943 and 1944 were the result of the 1943 epidemic that all but exterminated the stock (Van Oosten 1947). Production recovered slowly in the ensuing years and exceeded a million pounds in 1949.

Total production: The combined catch of all species (fig. 15) rose from 2,319,000 pounds in 1929 to 2,924,000 pounds in 1931, declined to 1,418,000 pounds in 1933 and then increased five consecutive years to 4,004,000 pounds in 1938. A drop to

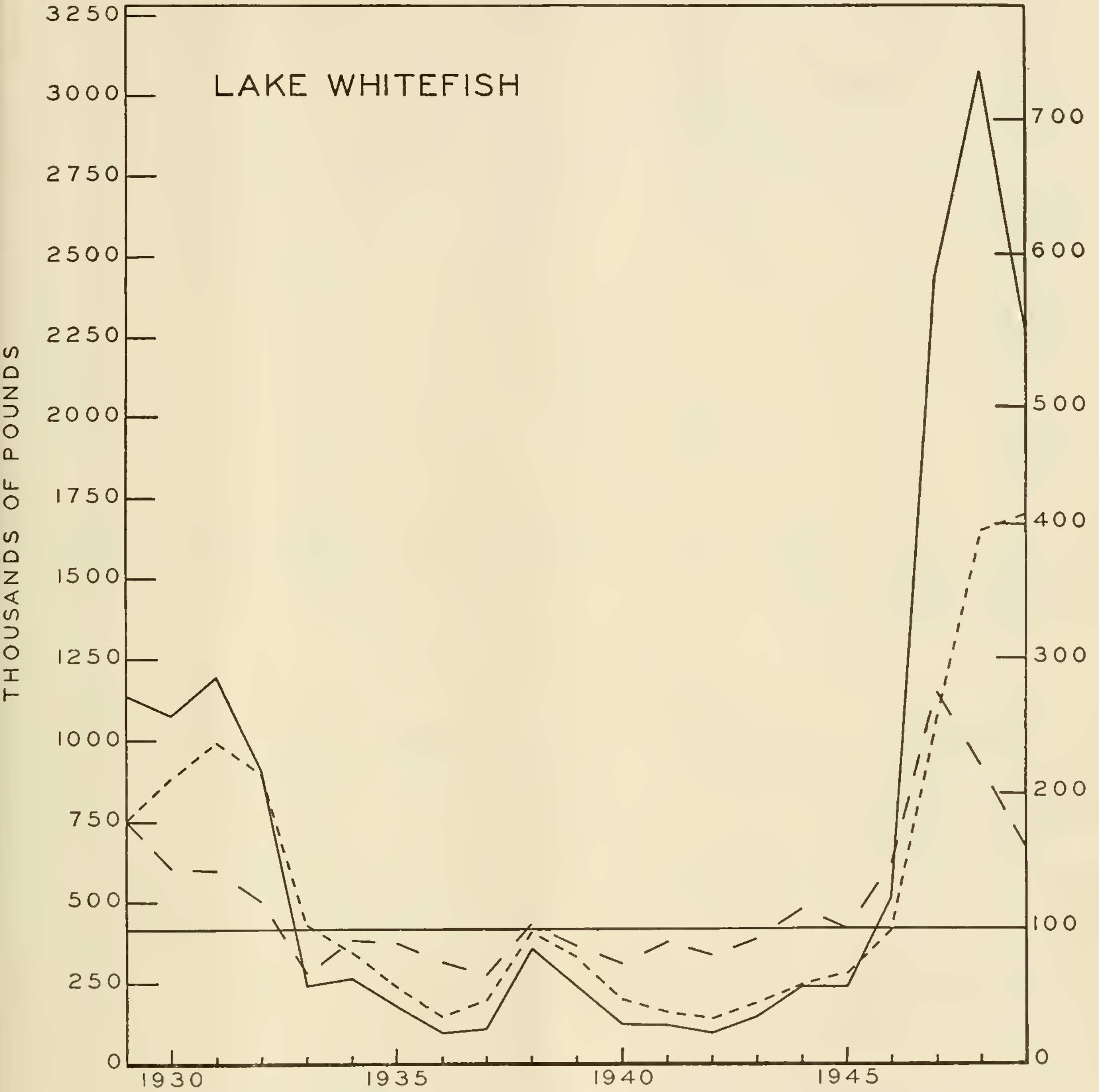

FIGURE 10.—Lake whitefish: Production (solid line), abundance (long dashes), and intensity of the fishery (short dashes) in State of Michigan waters of Green Bay, 1929–49, as percentages of the 1929–43 mean. Production is also given in pounds on scale at the left.

2,703,000 pounds in 1939 was followed by two more years in which the take exceeded 4 million pounds. From a peak of 4,319,000 pounds in 1941 the catch declined rapidly to the 21-year low of 1,379,000 pounds in 1944 only to rise in 4 years to the 21-year high of 7,909,000 pounds in 1948. The output was still high in 1949 (7,782,000 pounds).

The 1929–49 production statistics were characterized by the tendency for first one and then another of the four principal species of fish to dominate the catch. This dominance usually lasted 2 to 4 years. Whitefish, for example, contributed more than any other species to the catch during the 4 years, 1929–32, and the 3 years, 1947–49; the lake herring during the 4 years, 1936–39, and the 2 years, 1945–46; and the smelt during the 4 years, 1940–43. The only examples of dominance for a single year were provided by the lake

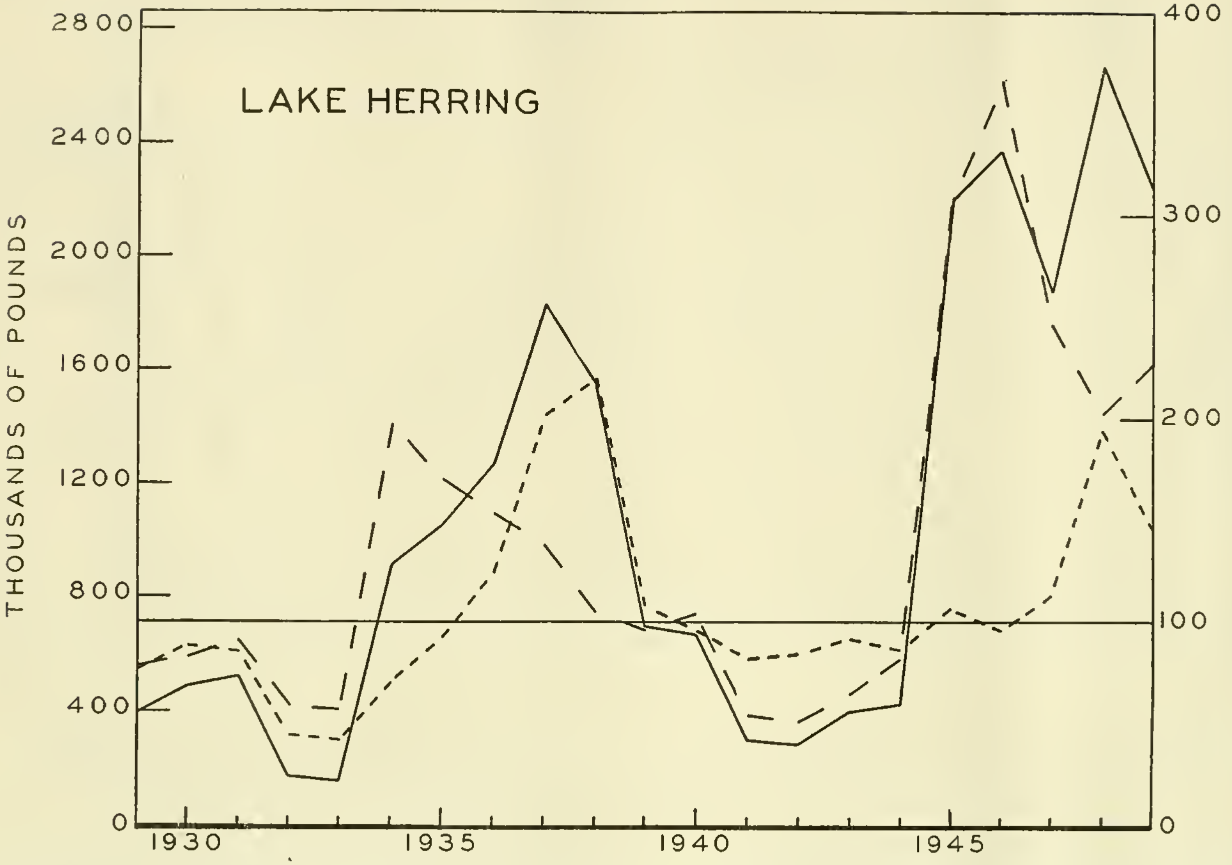

FIGURE 11.—Lake herring: Production (solid line), abundance (long dashes), and intensity of the fishery (short dashes) in State of Michigan waters of Green Bay, 1929–49, as percentages of the 1929–43 mean. Production is also given in pounds on scale at the left.

herring in 1934 and by the suckers in 1933, 1935, and 1944. These shifts of dominance were accompanied by relatively wide ranges in the percentage contribution of whitefish, lake herring, and smelt and can be related to the fluctuations of production described earlier. (It is to be noted that suckers, which exhibited no periodicity in production but rather showed erratic variations, failed to dominate the catch in consecutive years.)

Comparisons of production data for 1891–1908 and 1929–49 (tables 2, 4, and 6) reveal a much lower level of total yield in the latter period. The average annual output of 3,582,000 pounds for all species combined in 1929–49 was 3,503,000 pounds less than the 1891–1908 mean of 7,085,000 pounds—a decrease of 49.4 percent. Examination of the statistics for individual species shows that the decline in the production of lake herring alone more than accounted for this decrease. The catch of this species fell from 5,841,000 pounds in 1891–1908 to 1,070,000 pounds in 1929–49—a drop of 4,771,000 pounds, or 81.7 percent. For species other than lake herring the combined yield increased from 1,244,000 pounds in 1891–1908 to 2,512,000 pounds in 1929–49—an increase of 1,268,000 pounds, or 102.9 percent. Even if we exclude the smelt, an exotic variety not present in 1891–1908, the 1929–49 catch of fish other than lake herring was 52.5 percent greater than that of the earlier period. The greatest increase of production, aside from the introduced smelt, was that of whitefish (from 159,000 pounds in 1891–1908 to 714,000 pounds in 1929–49—a rise of 555,000 pounds, or 349.1 percent). The increase was large also for suckers (398,000 pounds in 1891–1908 and 699,000 pounds in 1929–49—a rise of 301,000 pounds, or 75.6 percent). These increases more than compensated the declines in the output of the remaining species (herring excluded) which were all less than 100,000 pounds (largest drop, lake

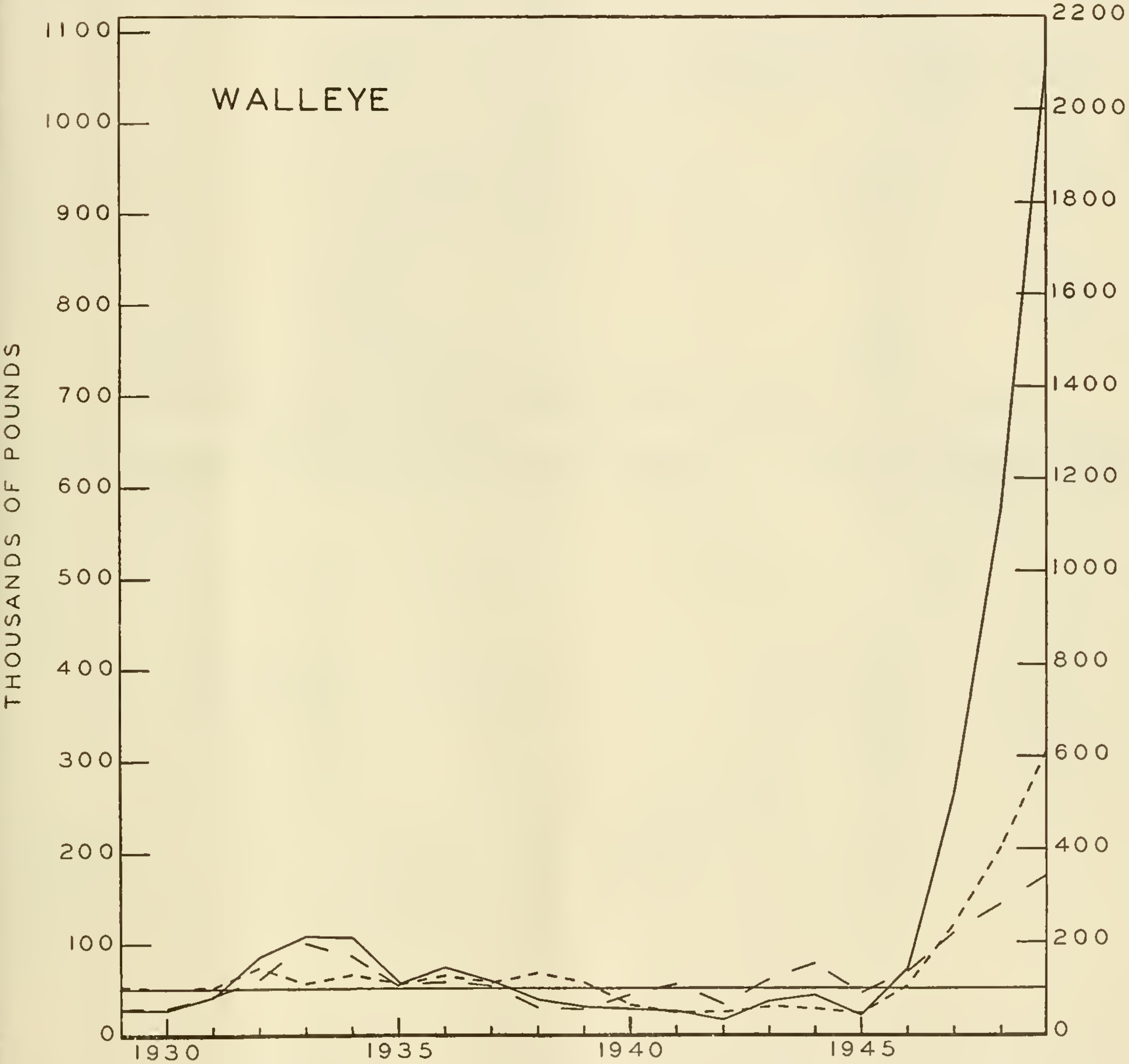

Figure 12.—Walleye: Production (solid line), abundance (long dashes), and intensity of the fishery (short dashes) in State of Michigan waters of Green Bay, 1929–49, as percentages of the 1929–43 mean. Production is also given in pounds on scale at the left.

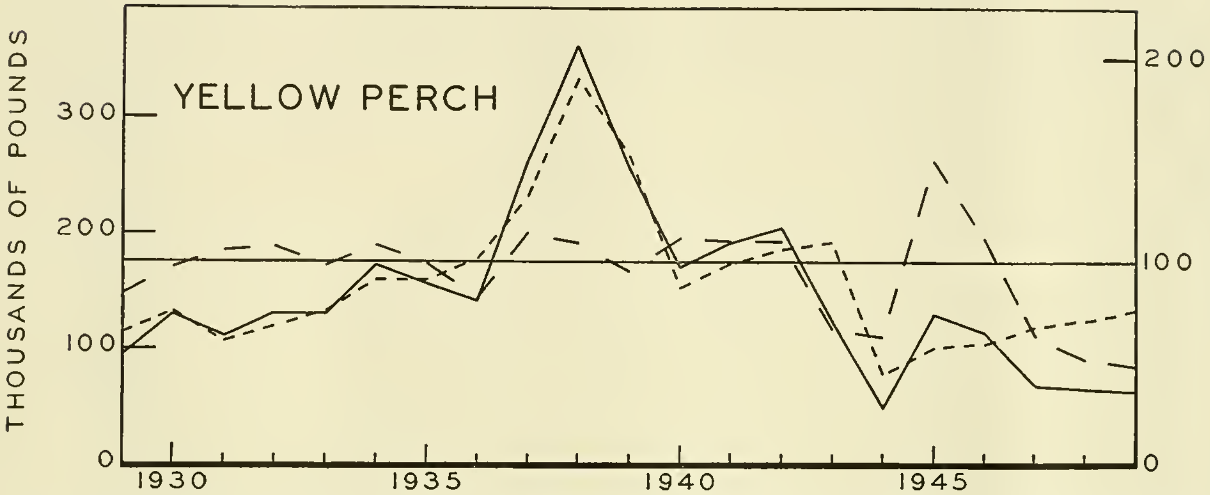

Figure 13.—Yellow perch: Production (solid line), abundance (long dashes), and intensity of the fishery (short dashes) in State of Michigan waters of Green Bay, 1929–49, as percentages of the 1929–43 mean. Production is also given in pounds on scale at the left.

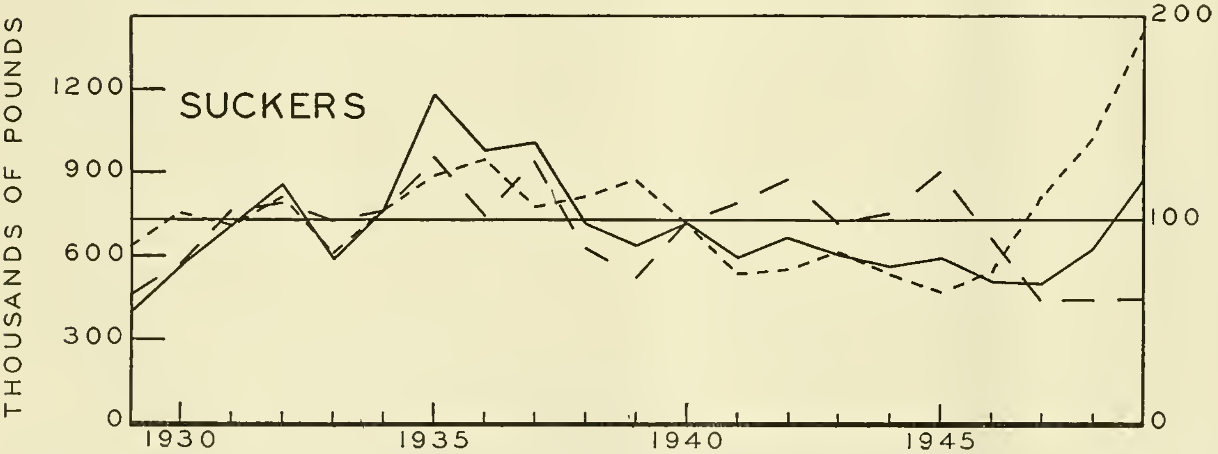

Figure 14.—White and redhorse suckers: Production (solid line), abundance (long dashes), and intensity of the fishery (short dashes) in State of Michigan waters of Green Bay, 1929–49, as percentages of the 1929–43 mean. Production is also given in pounds on scale at the left.

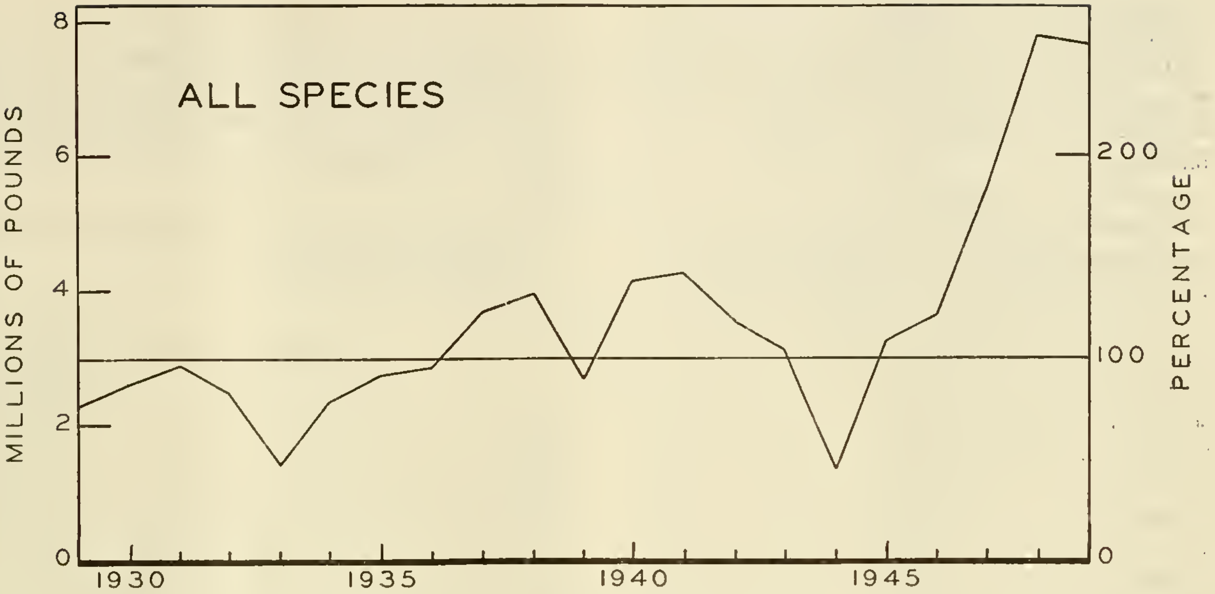

FIGURE 15.—All species: Commercial production in State of Michigan waters of Green Bay, 1929–49, in millions of pounds and as percentages of the 1929–43 mean.

trout—87,000 pounds), and except for the sturgeon [5] did not exceed 40.8 percent (the figure for the lake trout).

TABLE 6.—*Comparison of production in the commercial fisheries of Green Bay, by species, 1891–1908 and 1929–49*

Species	Production in 1891–1908		Production in 1929–49		Change from 1891–1908 to 1929–49		
	Thousands of pounds	Percentage of total	Thousands of pounds	Percentage of total	Thousands of pounds	Percentage of total	Percentage change in production
Lake trout	213	3.0	126	3.5	−87	0.5	−40.8
Whitefish	159	2.3	714	19.9	555	17.6	319.1
Lake herring	5,841	82.4	1,070	29.9	−4,771	−52.5	−81.7
Walleye	197	2.8	133	3.7	−64	.9	−32.5
Yellow perch	157	2.2	150	4.2	−7	2.0	−4.5
Suckers [1]	398	5.6	699	19.5	301	13.9	75.6
Smelt	--------	------	624	17.4	624	17.4	--------
Lake sturgeon	22	.3	--------	------	−22	−.3	--------
Others [2]	98	1.4	66	1.9	−32	.5	−32.7
All	7,085	100	3,582	100	−3,503	100	−49.4
All, except herring	1,244	17.6	2,512	70.1	1,268	52.5	102.9

[1] All suckers in 1891–1908; white and redhorse suckers in 1929–49.
[2] See tables 2 and 4 for list of species included.

The changes from 1891–1908 to 1929–49 in total production, in the take of the individual species, and in the species composition of the catch offer wide fields for speculation but the theories that can be advanced in explanation of these changes are mostly without supporting evidence. The shifts in production—increases of yield for some species and decreases for others—give prima facie evidence of changes in the conditions affecting the population as a whole, but we have little knowledge of the mechanisms whereby these changes came about. Fishing surely played an important role; however, it must have placed different degrees of pressure on different species and in turn the several species must have exhibited varying degrees of resistance to fishing pressure. Similarly, the effects of physical-chemical changes brought about by sawdust, bark, and other debris from the earlier lumbering period, by the varied industrial waste of the present era, by the fertilizing action of domestic sewage and of drainage from agricultural lands must have been significant and must have varied with the species of fish.

The differences from species to species in the direction of change in production from 1891–1908 to 1929–49 make any attempt to appraise the effects of fishing on the stocks especially difficult. Statistics on lake herring and whitefish illustrate the nature of the problem. It is inviting, for example, to explain the enormous drop in the production of lake herring from nearly 6 million pounds to barely 1 million pounds as depletion resulting from overexploitation. If this explanation is accepted, however, we are confronted at once with the problem of accounting for the simultaneous increase (from 159,000 pounds to 714,000 pounds) in the average annual take of whitefish—a species much higher priced than the lake herring, always in market demand, and continually subject to intensive fishing.

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[5] The taking of sturgeon became illegal in 1929.

Seemingly paradoxical situations such as the one just described become less perplexing if we admit the concept that in mixed stocks of the type found in Green Bay and other shallow-water areas of the Great Lakes (that is, stocks in which several species not closely related and of different habits are present in number) the effects of fishing should be considered in terms of the entire population rather than individual species, and recognize that a major effect of fishing lies in the disturbance of ecological relations among the fishes. Thus, fishing pressure to which the species are subject in common may give one a competitive advantage and place another at a disadvantage. Differences of fecundity, growth, and longevity, . . . that lead to a particular species composition at one level of fishing intensity may bring about a greatly different composition at another. Changes of this origin can be accentuated if fishing pressures, relative to the actual stock, differ from species to species. Furthermore, the generally lower level of commercial production in the modern period suggests the possibility that fishing pressure on commercially exploited species may have operated so much to the advantage of the smaller, noncommercial species that the latter now make up an increased percentage of the total biological production.

SEASONAL TRENDS OF PRODUCTION AND COMPOSITION OF THE CATCH ACCORDING TO GEAR

The statistics on seasonal trends of production (tables 7 and 8) and on the gear composition of the catch (table 9) of the principal species in State of Michigan waters of Green Bay were based on the records for 1929–49. The presentation of these data for the 1929–43 base period would be little to the point since we are concerned here with average conditions and not with trends of annual fluctuation about a norm. Seasonal trends and gear composition both varied considerably from year to year, but the expansion of the tabular material to show these variations is not justified.

SEASONAL DISTRIBUTION OF THE CATCH

The data on monthly and quarterly trends of production for five of the seven species listed in tables 7 and 8 were affected materially by closed seasons. These seasons as presently defined by Michigan State law [6] are as follows (seasons open and close at noon on the dates indicated): Lake trout, October 10–November 10; whitefish, November 5–December 10; walleye, April 1–May 20;

Table 7.—*Percentage distribution, by month and quarter, of the average annual catch of the principal species of fish in Green Bay, 1929–49*

Period of time	Lake trout	White-fish	Lake herring	Wall-eye	Yel-low perch	White and red-horse suckers	Smelt
Month:							
Jan	3.6	5.6	5.3	6.4	6.8	11.9	12.0
Feb	4.1	6.2	11.6	3.9	4.6	7.9	33.2
Mar	6.1	4.1	8.4	6.2	3.5	10.1	46.2
Apr	26.2	8.4	.4	.3	2.8	11.7	6.7
May	16.5	16.4	3.9	14.6	2.3	11.9	.2
June	7.3	12.0	12.3	19.7	3.3	9.9	.4
July	5.7	6.3	6.5	5.7	3.3	6.8	.2
Aug	9.8	5.1	2.5	5.5	5.4	5.7	.1
Sept	8.7	8.8	1.8	12.1	11.1	7.0	.2
Oct	5.6	14.9	7.7	13.4	22.1	5.0	.2
Nov	4.2	5.3	29.9	6.4	20.1	3.2	.3
Dec	2.2	6.9	9.8	5.8	14.7	8.9	.3
Quarter:							
First	13.8	15.9	25.2	16.5	14.9	29.9	91.4
Second	50.0	36.8	16.6	34.6	8.4	33.5	7.3
Third	24.2	20.2	10.8	23.3	19.8	19.5	.6
Fourth	12.0	27.1	47.4	25.6	56.9	17.1	.8

Table 8.—*Distribution, by month and quarter, of the average catch of the principal species of fish in Green Bay, 1929–49*

[In thousands of pounds]

Period of time	Lake trout	White-fish	Lake herring	Wall-eye	Yel-low perch	White and red-horse suckers	Smelt
Month:							
Jan	4.5	40.0	56.9	8.5	10.3	83.4	74.7
Feb	5.2	44.2	123.4	5.2	6.8	55.5	207.3
Mar	7.7	29.4	89.2	8 2	5.2	70.2	288.1
Apr	33.0	59.7	4.7	.4	4.2	81.9	41.9
May	20.8	116.9	41.8	19.5	3.5	83.1	1.0
June	9.2	85.9	131.5	26.2	4.9	69.2	2.3
July	7.2	45.4	69.7	7.6	4.9	47.5	1.3
Aug	12.4	36.4	26.2	7.3	8.1	39.8	.9
Sept	11.0	62.6	18.9	16.1	16.7	48.9	1.3
Oct	7.1	106.2	82.8	17.9	33.2	34.6	1.2
Nov	5.2	37.9	319.7	8.5	30.1	22.6	1.6
Dec	2.7	49.3	105.1	7.7	22.0	61.9	2.1
Quarter:							
First	17.3	113.6	269.5	21.8	22.3	209.1	570.1
Second	63.0	262.5	178.0	46.0	12.6	234.3	45.3
Third	30.6	144.4	114.8	31.1	29.7	136.2	3.6
Fourth	15.1	193.3	607.6	34.1	85.3	119.1	4.9
Total	126.0	713.9	1,069.8	133.0	149.9	698.7	623.7

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[6] Some adjustments have been made in the closed seasons since 1928, but a detailed account of these changes does not seem desirable.

yellow perch, April 15–May 20; suckers, April 15–May 15. The depressing effects of these closed seasons is especially strong because they cover approximately the spawning periods of the several species and prevent capture of the fish at a time when they are particularly easy to take. Lake herring and smelt are not subject to a closed season in State of Michigan waters of the Great Lakes.

Table 9.—*Average annual production and composition of the catch, by gear, of the principal species of fish in Green Bay, 1929–49*

[In thousands of pounds]

Species	Gill nets[1]			Pound nets	Shallow trap nets	Fyke and hoop nets	Set hooks	Other[2]	Total
	Bait	Small-mesh	Large mesh						
Lake trout:									
Production	----------	0.1	104.4	7.1	0.1	[3]0	11.5	2.8	126.0
Percentage	----------	.1	82.9	5.6	.1	[4]0	9.1	2.2	----------
Whitefish:									
Production	----------	0	438.7	245.1	4.1	1.0	----------	25.0	713.9
Percentage	----------	0	61.5	34.3	.6	.1	----------	3.5	----------
Lake herring:									
Production	0.3	516.3	3.3	534.1	10.3	3.8	----------	1.7	1,069.8
Percentage	[4]0	48.2	.3	49.9	1.0	.4	----------	.2	----------
Walleye:									
Production	----------	.2	32.7	25.3	49.1	23.9	[3]0	1.9	133.0
Percentage	----------	.1	24.6	19.0	36.9	18.0	[4]0	1.4	----------
Yellow perch:									
Production	[3]0	92.1	.2	4.2	32.5	20.0	.2	.7	149.9
Percentage	[4]0	61.5	.1	2.8	21.7	13.3	.1	.5	----------
White and redhorse suckers:									
Production	[3]0	1.2	151.9	64.1	394.0	80.8	----------	6.6	698.7
Percentage	[4]0	----------	21.7	9.2	56.4	11.6	----------	.9	----------
Smelt:									
Production	100	6.9	3.4	503.1	.3	5.1	----------	4.4	623.7
Percentage	16.1	1.1	.6	80.7	[4]0	.8	----------	.7	----------

[1] Mesh sizes, extension measure: Bait nets, mostly 1½–1⅝ inches; small-mesh nets, 2¼–2¾ inches; large-mesh nets, 4½ inches and larger.

[2] Includes catches by deep trap nets (not fished after 1935), dip nets, hand lines, and trolling; also catches for which records of gear were lacking (no catches in this category after 1937).

[3] Less than 50 pounds.

[4] Less than 0.05 percent.

Inasmuch as seasonal trends are of principal interest in this section (actual production of the important species was discussed in the preceding section), the following brief comments on the monthly and quarterly distribution of the catch are based on the percentages of table 7.

Lake trout: The contribution to the average annual total exceeded 10 percent in only 2 months—April (26.2 percent) and May (16.5 percent). The percentages were less than 5.0 during January and February and November and December and ranged from 5.6 to 9.8 in the remaining months. The figures by quarters show that half (50.0 percent) of the annual production took place in the spring[7] and a little less than a fourth (24.2 percent) in the summer. Production was lowest in the first (13.8 percent) and fourth (12.0 percent) quarters.

Whitefish: The monthly and quarterly distributions of the catch were more nearly even in the whitefish than in the lake trout. The maximum percentage for any single month was 16.4 (May) and in only one month did the percentage fall below 5 (4.1 in March). The spring quarter was the most productive (36.8 percent) and the winter quarter the poorest (15.9 percent). Values for the third (20.2 percent) and fourth (27.1 percent) quarters did not deviate greatly from the expected figure of 25.

Lake herring: The percentage for November (29.9), the month in which much of the spawning occurs, was far greater than that for any other month. Among the remaining 11 months the percentage exceeded 10 in only 2 (12.3 in June and 11.5 in February), and fell below 5 in 4 (lowest value, 0.4 in April). The most productive quarter by far was the fourth (47.4 percent) and the poorest was the third (10.8 percent).

Walleye: The most productive months were June (19.7 percent) and May (14.6 percent), with October (13.4 percent) and September (12.1 percent) not far behind. If April, which in recent years has been completely closed to walleye fishing, is excluded the figures for the remaining months range from 6.4 percent in January and November to 3.9 percent in February. The best quarter was the second (34.6 percent) and the least productive was the first (16.5 percent). The percentages for both the summer (23.3) and autumn (25.6) quarters were near the 25-percent level.

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[7] In this section, winter, spring, summer, and autumn are treated as synonymous with the first, second, third, and fourth quarters.

Yellow perch: The three most productive months (October, 22.1 percent; November, 20.1 percent; December, 14.7 percent) fell in the autumn. Production was good in September also (11.1 percent), but in the remaining months the percentage did not exceed 6.8 (the figure for January) and was as low as 2.3 (May). More than half (56.9 percent) of the average annual total was produced in the fourth quarter and more than three-fourths (76.7 percent) in the second half of the year. The winter (14.9 percent) and spring (8.4 percent) quarters together accounted for less than a fourth (23.3 percent) of the annual take.

White and redhorse suckers: With the exception of November which contributed only 3.2 percent of the average annual total, the percentages for the individual months did not fall below 5.0 (the figure for October) or exceed 11.9 (the value for January and May). Most productive quarters were the second (33.5 percent) and first (29.9 percent), but contributions of the summer and autumn quarters (19.5 and 17.1 percent, respectively) were nevertheless substantial.

Smelt: The major production of smelt comes from the winter ice fishing. March alone accounted for 46.8 percent of the 1929–49 commercial take, and February for almost a third (33.2 percent). The combined percentage for the three winter months was 91.4. The percentage was 6.7 for April but in none of the remaining 8 months did the value exceed 0.4 (the figure for June).

Actually, large catches of smelt dipped from tributary streams during the spawning period (mostly in April) and not recorded in fishing reports find their way into commercial channels. No exact measure of the quantities of smelt taken during the spawning run is available but a good idea of the magnitude of the catch is provided by the estimate of the Michigan Department of Conservation that dippers took more than 5½ million pounds from State of Michigan waters in 1942 (Van Oosten 1947). A large portion of this catch was taken in the Green Bay area, which is the center of greatest abundance of smelt. By no means all of the smelt captured by dippers are sold. Much of the catch is consumed by the dippers, their families, and friends and a certain amount is wasted, but enough is sold to bring about a complete collapse of the market in years of high abundance.

GEAR COMPOSITION OF THE CATCH

The data of table 9 on the composition of the catch of the important species according to gear bring out two major points: All species were produced in quantity by more than one kind of gear, and most of the principal gears produced significant amounts of more than one species of fish.

For the different species the most important gears and the percentage contribution of each to the average annual total for the species were as follows (no percentages less than 5.0 listed):

Lake trout: Large-mesh[8] gill nets, 82.9; set hooks, 9.1; pound nets, 5.6.

Whitefish: Large-mesh gill nets, 61.5; pound nets, 34.3.

Lake herring: Small-mesh gill nets, 48.2; pound nets, 49.9.

Walleye:[9] Shallow trap nets, 36.9; large-mesh gill nets, 24.6; pound nets, 19.0; fyke and hoop nets, 18.0.

Yellow perch: Small-mesh gill nets, 61.5; shallow trap nets, 21.7; fyke and hoop nets, 13.3.

White and redhorse suckers: Shallow trap nets, 56.4; large-mesh gill nets, 21.7; fyke and hoop nets, 11.6; pound nets, 9.2.

Smelt: Pound nets, 80.7; bait nets,[10] 16.1.

Average annual production of important species in thousands of pounds by the principal gears was as follows (except for fyke nets and set hooks no catches less than 25.0 listed):

Bait nets: Smelt, 100.6.

Small-mesh gill nets: Lake herring, 516.3; yellow perch, 92.1.

Large-mesh gill nets: Whitefish, 438.7; suckers, 151.9; lake trout, 104.4; walleye, 32.7.

Pound nets: Lake herring, 534.1; smelt, 503.1; whitefish, 245.1; suckers, 64.1; walleye, 25.3.

Shallow trap nets: Suckers, 394.0; walleye, 49.1; yellow perch, 32.5.

Fyke and hoop nets: Suckers, 80.8; walleye, 23.9; yellow perch, 20.0.

Set hooks: Lake trout, 11.5.

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[8] See footnote 1 to table 9 for statement of mesh sizes for the different types of gill nets.

[9] The sudden rise in production of walleyes to unprecedentedly high levels in recent years was accompanied by a pronounced shift in gear composition of the catch as the following percentages for the 1929–43 base period prove: Fyke and hoop nets, 50.2; pound nets, 24.9; shallow trap nets, 20.2; large-mesh gill nets, 3.6.

[10] The term "bait net" derives from the traditional use of the gear for the capture of small chubs and lake herring as bait for set hooks fished for lake trout.

FLUCTUATIONS IN ABUNDANCE OF THE PRINCIPAL SPECIES OF GREEN BAY, 1929–49

The abundance, or availability, indices[11] of table 10 were derived from the records of catch per unit of effort of tables 11 to 16 by methods described in publications listed in the introduction of this paper (Hile, 1937, gave an example of the actual computations). Information on the catch per unit of effort is given for smelt in table 17, but no attempt has been made to compute abundance percentages for the species. The comparatively recent development of the smelt fishery and the disruption occasioned by the 1943 mortality have prevented the establishment of satisfactory norms.

TABLE 10.—*Abundance indices of six commercially important fish in Green Bay, 1929–49*

[Expressed as percentages of the 1929–43 mean]

Year	Lake trout	White-fish	Lake herring	Walleys	Yellow perch	White and red-horse suckers
1929	71	180	78	54	84	63
1930	65	145	83	57	97	78
1931	69	143	91	83	105	104
1932	80	120	58	121	107	108
1933	97	66	57	198	98	99
1934	92	91	197	171	108	104
1935	87	89	170	106	99	131
1936	137	75	153	115	82	102
1937	157	65	138	105	114	129
1938	112	104	105	57	109	86
1939	94	86	96	54	98	71
1940	105	74	104	86	112	99
1941	138	90	54	108	110	108
1942	96	80	51	66	110	120
1943	100	92	65	119	67	98
1944	53	114	82	152	63	103
1945	51	100	306	89	150	124
1946	32	148	367	136	112	91
1947	26	275	217	[1] 220	64	60
1948	44	221	203	[1] 282	53	61
1949	45	158	228	[1] 344	49	61

[1] Probably too high; see text, p. 22.

TABLE 11.—*Catch, in pounds, of lake trout per unit of effort in Green Bay, by gear, 1929–49*

[Per lift of 10,000 linear feet of large-mesh gill nets, of one pound net, and of 1,000 set hooks]

Year	Large-mesh gill nets	Pound nets	Set hooks
1929	66	14	223
1930	57	15	253
1931	63	13	201
1932	78	18	151
1933	106	16	197
1934	73	29	247
1935	79	23	237
1936	168	8	165
1937	189	13	154
1938	121	16	129
1939	96	12	138
1940	118	8	129
1941	134	13	----------
1942	91	----------	102
1943	94	2	----------
Mean, 1929–43	102	[1] 14	[1] 184
1944	50	4	----------
1945	48	----------	----------
1946	30	----------	----------
1947	24	9	----------
1948	42	8	----------
1949	44	5	----------

[1] When data were lacking for one or more years the 15-year average was estimated by dividing the mean of the available annual averages by the mean of the abundance percentages for the same years. See Van Oosten, Hile, and Jobes (1946) for comments on the estimation of a normal catch when data are not available for all years.

TABLE 12.—*Catch, in pounds, of whitefish per unit of effort in Green Bay, by gear, 1929–49*

[Per lift of 10,000 linear feet of large-mesh gill nets, of one pound net, and of one deep trap net]

Year	Large-mesh gill nets	Pound nets	Deep trap nets[1]
1929	183	113	----------
1930	150	89	132
1931	131	104	100
1932	116	74	118
1933	71	41	55
1934	100	56	75
1935	105	42	91
1936	77	48	----------
1937	72	38	----------
1938	120	54	----------
1939	74	63	----------
1940	83	44	----------
1941	125	39	----------
1942	92	39	----------
1943	102	43	----------
Mean, 1929–43	107	59	[2] 87
1944	123	60	----------
1945	110	52	----------
1946	158	84	----------
1947	280	170	----------
1948	208	171	----------
1949	156	106	----------

[1] Became illegal during the 1935 season.
[2] Estimated. See footnote 1, table 11.

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[11] In using the terms "abundance" and "availability" interchangeably in references to our indices we follow Hile, Eschmeyer, and Lunger (1951a), rather than Marr (1951), when they stated:

> Arguments about which of the two words should be employed would constitute a futile quibbling over terminology. These estimates are based on the fishing experience of the fishermen—the records of their catch of legal-sized lake trout per standard unit of fishing effort. They offer no information on the abundance of undersized lake trout and are affected by such factors as meteorological conditions, annual differences in the time of spawning in relation to the fixed closed season, and annual differences in the distribution of fish. Yet, for all these obvious weaknesses they offer the best estimates of abundance to be had at the present time. Accordingly, we do not hesitate to use "availability" and "abundance" interchangeably.

TABLE 13.—*Catch, in pounds, of lake herring per unit of effort in Green Bay, by gear, 1929–49*

[Per lift of 10,000 linear feet of small-mesh gill nets and of one pound net]

Year	Small-mesh gill nets [1]	Pound nets
1929	614	88
1930	632	92
1931	622	113
1932	483	59
1933	507	54
1934	1,312	259
1935	1,241	208
1936	1,118	185
1937	926	205
1938	723	150
1939	651	143
1940	838	86
1941	437	26
1942	479	26
1943	343	146
Mean, 1929–43	728	123
1944	349	123
1945	154	498
1946	378	591
1947	1,526	329
1948	1,865	183
1949	2,062	195

[1] About 2¼ to 2¾ inches, extension measure.

TABLE 14.—*Catch, in pounds, of walleye per unit of effort in Green Bay, by gear, 1929–49*

[Per lift of one pound net, of one shallow trap net, and of one fyke net]

Year	Pound nets	Shallow trap nets	Fyke nets
1929	11	4	15
1930	7	5	20
1931	11	10	27
1932	20	10	37
1933	33	19	57
1934	32	9	59
1935	35	5	31
1936	62	7	23
1937	20	10	30
1938	8	4	20
1939	8	2	23
1940	10	8	28
1941	9	11	32
1942	9	4	23
1943	11	7	54
Mean, 1929–43	19	8	32
1944	13	13	58
1945	6	17	20
1946	8	21	23
1947	17	30	48
1948	28	40	66
1949	27	56	57

TABLE 15.—*Catch, in pounds, of yellow perch per unit of effort in Green Bay, by gear, 1929–49*

[Per lift of 10,000 linear feet of small-mesh gill nets, of one shallow trap net, and of one fyke net]

Year	Small-mesh gill nets	Shallow trap nets	Fyke nets
1929	262	6	18
1930	273	8	17
1931	239	20	17
1932	233	21	17
1933	212	18	14
1934	241	17	22
1935	298	13	16
1936	205	12	13
1937	309	17	16
1938	306	12	17
1939	308	8	16
1940	378	7	18
1941	302	11	14
1942	281	14	19
1943	170	7	17
Mean, 1929–43	268	13	17
1944	191	5	7
1945	404	6	22
1946	339	4	17
1947	198	5	11
1948	186	4	17
1949	185	4	8

TABLE 16.—*Catch, in pounds, of white and redhorse suckers per unit of effort in Green Bay, by gear, 1929–49*

[Per lift of 10,000 linear feet of large-mesh gill nets, of one pound net, of one shallow trap net, and of one fyke net]

Year	Large-mesh gill nets	Pound nets	Shallow trap nets	Fyke nets
1929	102	45	59	46
1930	156	51	63	54
1931	167	68	108	55
1932	232	61	96	61
1933	251	80	69	65
1934	434	46	68	96
1935	431	63	117	62
1936	420	43	85	49
1937	723	47	98	73
1938	365	36	73	44
1939	338	36	56	40
1940	398	31	83	61
1941	504	16	86	75
1942	400	7	110	81
1943	404	28	74	149
Mean, 1929–43	355	44	83	67
1944	387	35	73	116
1945	378	27	104	95
1946	175	36	86	91
1947	140	30	51	71
1948	159	28	50	71
1949	170	17	55	59

TABLE 17.—*Catch, in pounds, of smelt per unit of effort in Green Bay, by gear, in each of the months, January to April, 1938–49*

[Per lift of 1,000 linear feet of small-mesh gill nets (bait nets) and of one pound net]

Year	Small-mesh gill nets [1]				Pound nets			
	Jan.	Feb.	Mar.	Apr.	Jan.	Feb.	Mar.	Apr.
1938	67	68	117	214	233	175	182	-------
1939	50	76	128	223	267	207	474	1,173
1940	45	60	74	110	347	365	544	1,252
1941	68	59	95	233	353	378	472	391
1942	-------	57	88	-------	225	313	447	869
1943	67	62	37	-------	374	211	34	-------
1944	-------	-------	-------	-------	-------	-------	-------	-------
1945	-------	-------	-------	-------	13	23	50	68
1946	29	43	58	-------	6	20	43	40
1947	-------	37	56	204	83	66	104	659
1948	43	39	48	158	139	114	102	594
1949	28	54	52	125	157	182	347	1,129

[1] Mesh sizes mostly 1½ to 1⅝ inches, extension measure.

Comparison of the annual fluctuations in the catch of a particular species per unit effort of different gears reveals that major improvements or declines in the success of fishing commonly were shared by the principal types of nets[12] but that certain discrepancies occurred. Numerous examples can be found in which the catch per lift of one gear increased over that of the previous year while the catch of another gear exhibited a decline. Furthermore, the relative increases or decreases of different gears were often dissimilar even when there was agreement as to direction of change. Some of these discrepancies doubtless reflect inadequacies (and to some extent inaccuracies) of the original data. On the other hand, extremely close agreement between the annual fluctuations in the catch per unit of effort of a species in different gears was not to be expected.

One important source of discrepancies between trends in the catch of different gears most probably lies in annual differences in the distribution of fish as related to hydrographic and other ecological conditions. One year these conditions may tend to concentrate the fish on grounds fished principally by one gear and cause them to be scarce on the major grounds of another, whereas the next season the situation may be reversed. We are not in position to offer quantitative information on this point, but we do know from general observations on the fishery and from statements of fishermen that different gears fished on different grounds do not share equally increases or decreases in the abundance of fish.

A second factor contributing to the discrepancies between trends in the catch of different gears is that some gears operate most effectively over certain size ranges. Thus a progressive change in the size composition of the stock may operate to the advantage of first one and then another type of net. Records for the lake herring (table 13) provide a good example of this type of disagreement. From 1929 through the middle 1930's, fluctuations in the catch of herring per unit effort of small-mesh gill nets and pound nets, although by no means identical, were generally similar. This situation changed during the late 1930's and early 1940's with the development and widespread use of pound nets with extremely small meshes (about 1½ inches extension measure, as manufactured, and still smaller after treatment with preservative). This new type of pound net was designed for smelt but proved so efficient at taking small or "pin" herring, that with its general use changes in the abundance of that species became detectable in the pound-net catches before they were noticed by gill netters who take larger fish. The relatively poor pound-net lifts of 1940–42, for example, were followed by poor gill-net fishing in 1943–46. Again, the rich 1943 year class led to large catches of "pins" as early as 1945 whereas the catch per unit effort of gill nets did not rise sharply until 1947. In this situation both gears probably offered fair indication of the abundance of fish of the size they took but they fished different size groups within the general population.

From the considerations of the preceding two paragraphs it appears first, that discrepancies between gears in the annual fluctuations in the catch per lift of a particular species do not necessarily mean weakness of the data; and second, that the procedure followed in our statistical studies of pooling the data from different gears to obtain our abundance index probably gives the best estimate of abundance of fish of commercial size to be had at the present time.

The abundance percentages for all six species listed in table 10 exhibited rather wide fluctuations and in some species these fluctuations tended to be periodic. The following brief statements concerning trends for the different species can be followed more easily if reference is made to figures 9 to 14.

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[12] The terms "gear" and "nets" are used interchangeably in this section since all fishing apparatus with which we are concerned fall under the category of "nets" except the set hooks formerly fished for lake trout.

Lake trout: During earlier years of the 1929–49 period, abundance was generally below the 15-year (1929–43) mean but the trend was irregularly upward (fig. 9). Sharp increases in 1936 and 1937 carried the index to the 21-year maximum of 157 in 1937. A decline to 94 in 1939 was followed by a rise to a second peak of 138 in 1941. The succeeding years saw a pronounced downward trend which culminated in an index of only 26 in 1947. The rise to 44 in 1948 and 45 in 1949 still left the abundance far below average. The recent decline of the lake trout can be attributed primarily to the depredations of the sea lamprey (Hile, Eschmeyer, and Lunger 1951a).

Whitefish: Van Oosten, Hile, and Jobes (1946) believed that 1929 represented the peak year of a period during which whitefish were abnormally plentiful in Lake Michigan. In Green Bay the 1929 index stood at 180 (fig. 10). From this value the abundance declined to 66 in 1933, recovered somewhat in 1934 (91), and then declined to the 21-year low (65) in 1937. After this year the availability of whitefish entered on a definite, though slightly irregular, upward trend. Large increases from 100 in 1945 to 148 in 1946 and the 21-year maximum of 275 in 1947 were followed by substantial declines to 221 in 1948 and 158 in 1949.

Lake herring: The abundance was consistently below average in 1929–33 (range from 57 in 1933 to 91 in 1931—see fig. 11). A sharp increase to 197 in 1934 was followed by a long decline (interrupted by a small rise in 1940) that led to the 21-year low of 51 in 1942. Small increases in 1943 and 1944, a phenomenal jump from 82 to 306 in 1945, and yet another increase to 367 in 1946, raised the level of abundance to the 21-year high. The subsequent downward trend which carried the percentage to 203 in 1948 was halted by a rise to 228 in 1949.

Walleye: From the 21-year minimum of 54 in 1929 the abundance of walleyes (fig. 12) rose to 198 in 1933 and then fell away to the same minimum of 54 in 1939 (interruption to the decline in 1930). The following years saw a highly irregular but definite upward trend. The increases were so large after 1946 that a level of 344 was reached by 1949.

The data on the catch of walleyes per lift (table 14) together with our knowledge of changes that have taken place in the types of trap nets fished in Green Bay give us reason to suspect that the abundance of walleyes during the last few years, particularly in 1947–49, may have been overestimated. The catches per lift of fyke nets in these 3 years indicate a great abundance of walleyes (catches from 150 to 206 percent of the 1929–43 mean) and the pound-net records for 1948 and 1949 support a similar view (lifts 147 and 142 percent of 1929–43 mean). These 1947–49 figures were relatively far lower, however, than those for trap nets in which the average lift ranged from 30 to 56 pounds as compared with a 15-year average of 8. To some extent this relatively greater increase in the catch of trap nets may have reflected especially heavy concentrations of fish on trap-net grounds (as compared with pound-net and fyke-net grounds) during the years of high abundance of walleyes. Much of the exceptional success of trap nets, however, is believed to have resulted from the introduction (especially by Lake Huron fishermen who moved into the area) of larger nets better suited to the taking of walleyes than the gear employed by local operators in earlier years.

Yellow perch: During the years 1929–42, fluctuations in the abundance of yellow perch (fig. 13) were largely without trend and relatively limited (ranged from 82 in 1936 to 114 in 1937), but during the later years the variations were wide. After dropping from 110 in 1942 to 63 in 1944 the abundance index jumped suddenly to the 21-year peak of 150 in 1945 only to fall away to the 21-year low of 49 in 1949.

White and redhorse suckers: The fluctuations in abundance of suckers (fig. 14), much like those of yellow perch, were without clear-cut trends. The index was low (63) in 1929, but during the next 17 years it varied irregularly within the range of 71 (1939) to 131 (1935). The level of availability was again low (60 or 61) during the last 3 years, 1947–49.

Smelt: As stated earlier, late development of the fishery and the effects of the 1943 epidemic have prevented the establishment of "normal" standards from which to estimate annual fluctuations in the abundance of smelt; nevertheless, a good idea of the extent of these fluctuations is to be had from the records of the catch per unit effort for the months January to April (table 17). Particular attention should be given to the figures for January, February, and March, the 3 months of highest production (tables 7 and 8). Annual fluctuations in the catch per net during these months exhibited no pronounced trend prior to 1943. In that year the January-February catches of gill nets and the January catches of pound nets gave no inkling of the unusual events to come, but in February the catch of smelt per pound net was the lowest since 1939. This decrease is to be associated with the mortality which Van Oosten (1947) believed to have started about the middle of February. By March 1943 the fishery was in a state of collapse. Almost no smelt were taken in 1944 and production (table 4) and catch per net (table 17) both were low in 1945 and 1946. In 1947–49 both production and the catch per unit effort exhibited an upward trend that bids fair to carry the fishery soon to the premortality level.

Examination of table 10 gives strong indication that the annual fluctuations in availability of certain species tended to be similar, whereas with others the trends were distinctly opposite. To bring out these relationships more clearly coefficients of correlation (*r*) between abundance percentages have been computed for all pairings of the six species (table 18). In these calculations all coefficients involving lake trout were restricted to the 15-year period, 1929–43, since it is believed that the abundance of that species has not followed "natural" fluctuations in recent years but rather has been controlled by depredations of the sea lamprey. All other coefficients were based on the 21-year interval.

Of the 15 coefficients listed in table 18, 7 were significant at the 5-percent level of probability (p); 6 of these 7 were "highly significant" ($p<0.01$). Thus we have strong evidence that the fluctuations in abundance of several of the species were in fact correlated. It would be futile at this time to speculate how these relationships came about—whether they represent interreactions between species, similar or opposite reactions to changing ecological conditions . . . Before we can hope to improve greatly our understanding of the changes within the fish populations in northern Green Bay we must increase our knowledge of the biology of the various species; nevertheless, data of the type given in table 18 can be most helpful by suggesting lines of attack in the general research program.

TABLE 18.—*Correlations between fluctuations in abundance of lake trout and five other species, 1929–43, and among species other than lake trout, 1929–49*

[Absolute values of r corresponding to probabilities (*p*) of 0.1, 0.05, 0.02, 0.01, and 0.001, respectively, are 0.369, 0.433, 0.503, 0.549, and 0.665 for the 21-year interval and 0.441, 0.514, 0.592, 0.641, and 0.760 for the 15-year period]

Species	Lake trout	White-fish	Lake herring	Walleye	Yellow perch	White and red-horse suckers
Lake trout	--------	−0.690	0.205	0.187	0.181	0.426
Whitefish	−0.690	--------	.383	.459	−.534	−.726
Lake herring	.205	.383	--------	.402	.056	−.118
Walleye	.187	.459	.402	--------	−.645	−.582
Yellow perch	.181	−.534	.056	−.645	--------	.642
White and redhorse suckers	.426	−.726	−.118	−.582	.642	--------

Still further useful information can be had through an investigation of the correlations between abundance percentages for intervals shorter than the entire period for which data are at hand or after the establishment of a time lag of one or more years. This latter procedure can be justified logically since fish of different species hatched in the same year commonly do not enter the fishery simultaneously, and an abundance of large fish of a predator species may reduce stocks of prey species, . . . Examples of the results obtained from this type of analysis (table 19) bring out some interesting relationships. We have evidence, for example, that the correlation between the fluctuations in availability of whitefish and walleyes was negative in 1929–38, but that this situation was reversed in 1939–47 over which period the correlation was strongly positive. Equally striking are the data for the lake herring. Fluctuations in the abundance of this species were not correlated with those of other species when indices for the same calendar year were paired but exhibited significant positive correlations with the abundance of walleyes 1, 2, or 3 years later or 1 or 2 years earlier, and significant negative correlation with the abundance of suckers 1 year later. Again, the expansion of the type of analyses illustrated in table 19 and the inquiry into the possible causes underlying the observed relationships must await further investigation of the natural histories of the various species.

TABLE 19.—*Correlations between annual fluctuations in abundance of fishes of northern Green Bay during specified intervals of time*

Abundance indices correlated	Period of time	r	p
Whitefish: Walleye	1929–38	−0.670	$0.05>p>0.02$
Whitefish: Walleye	1939–47	0.886	$0.01>p>0.001$
Whitefish: Yellow perch (1 year later)	1929–49	−0.533	$0.02>p>0.01$
Lake herring: Whitefish (1 year later)	1929–49	0.716	$0.001>p$
Lake herring: Walleye (1 year later)	1929–49	0.468	$0.05>p>0.02$
Lake herring: Walleye (2 years later)	1929–49	0.615	$0.01>p>0.001$
Lake herring: Walleye (3 years later)	1929–49	0.603	$0.01>p>0.001$
Lake herring: Suckers (1 year later)	1929–49	−0.467	$0.05>p>0.02$
Walleye: Lake herring (1 year later)	1929–49	0.481	$0.05>p>0.02$
Walleye: Lake herring (2 years later)	1929–49	0.567	$0.02>p>0.01$

As part of recent statistical studies of the lake trout fisheries of the Great Lakes, inquiries have been made into the dependability of production statistics as indicators (but not as measures) of fluctuations in abundance. Because of its bearing on the use of past data on production for judging changes of abundance that may have taken place, the accumulation of information on the dependability of estimation of abundance from production statistics is desirable. For no other waters of the Great Lakes are statistics on fishing intensity and, hence, on catch per unit effort available for a period as long as that in the State of Michigan (for all Great Lakes waters of the State beginning with 1929) and for certain States the collection of data on intensity of fishing began as recently as 1950. Analyses made to date support the general view that fluctuations of abundance are reflected in statistics of production but the exceptions bring out the need for caution in the interpretation of catch data and for a constant alertness to detect disturbing factors that may render those data useless or misleading.[13]

In northern Green Bay, fluctuations in production and abundance were correlated positively at significant levels (table 20) for four of six species (the value of r for yellow perch fell short of the 5-percent level in 1929–43 but was highly significant in 1929–49). For those fish, production served reasonably well as an indicator of changes in abundance. The lack of significant correlation in the data for lake trout (to be traced to a negative correlation between fishing intensity and the abundance of that species, see p. 25) demonstrates once more the need for caution in this use of catch statistics.

TABLE 20.—*Correlation between production and abundance indices for the principal commercial species in Green Bay, 1929–43 and 1929–49*

Species	1929–43		1929–49	
	r	p	r	p
Lake trout	−0.028	$p>0.10$	0.337	$p>0.10$
Whitefish	0.924	$0.001>p$	0.892	$0.001>p$
Lake herring	0.707	$0.01>p>0.001$	0.856	$0.001>p$
Walleye	0.869	$0.001>p$	0.878	$0.001>p$
Yellow perch	0.474	$0.10>p>0.05$	0.566	$0.01>p>0.001$
White and redhorse suckers	0.743	$0.01>p>0.01$	0.501	$0.05>p>0.02$

FLUCTUATIONS IN INTENSITY OF THE FISHERY FOR THE PRINCIPAL SPECIES OF GREEN BAY, 1929–49

An outstanding feature of the statistics on the 1929–49 fluctuations in the intensity of the fishery for the principal species (table 21 and figs. 9 to 14) is the high level attained by most of the species during the later years of the period. For four of the six species (lake trout, lake whitefish, walleye,[14] and suckers), the 21-year maximum intensity was reached in 1948 or 1949, and for a fifth (lake herring) the intensity of the fishery in those 2 years was well above the 1929–43 mean. The intensity of the fishery for yellow perch was higher in 1948 and 1949 than in the years immediately preceding but was still below the 15-year average.

There is good evidence that the recent increase of fishing pressure on whitefish, lake herring, and walleye is to be associated with the nearly simultaneous rise in the abundance of those species (*cf.* tables 10 and 21). The increases in fishing intensity for lake trout and suckers, on the contrary, came about during periods of relatively low availability. These two exceptions indicate that a positive correlation between abundance and fishing intensity may not be the rule; such a view finds support in the data of table 22.

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[13] See Hile, Eschmeyer, and Lunger (1951a) for comments on the relation between fluctuations of abundance and production in Great Lakes fisheries.

[14] In the preceding section evidence was given that the estimates of abundance of walleyes were probably too high for recent years notably 1947–49. Our method of analysis is such that when abundance is overestimated, fishing intensity is underestimated correspondingly. Consequently the 1947–49 figures on fishing intensity for walleyes in table 21 are probably too low. It is not believed, however, that these underestimates impair the general validity of remarks in this section based on the intensity indices for walleyes.

TABLE 21.—*Fluctuations in fishing intensity for the principal commercial species in Green Bay, 1929–49*

[Expressed as percentages of the 1929–43 mean]

Year	Lake trout	White-fish	Lake herring	Walleye	Yellow perch	White and red-horse suckers
1929	162	180	76	104	65	87
1930	198	211	88	98	75	103
1931	204	238	85	102	61	97
1932	155	215	44	144	68	111
1933	88	102	42	111	75	83
1934	49	82	70	129	91	104
1935	56	56	92	108	91	121
1936	72	34	124	127	101	129
1937	94	46	197	112	132	106
1938	139	97	220	132	190	111
1939	105	78	108	112	152	119
1940	49	47	96	64	87	97
1941	35	37	82	48	99	73
1942	37	33	84	48	106	75
1943	57	44	92	61	107	84
1944	56	58	76	56	45	73
1945	36	66	107	46	58	64
1946	22	99	96	105	60	74
1947	111	251	113	[1] 236	63	111
1948	253	395	195	[1] 403	72	140
1949	207	407	145	[1] 615	77	194

[1] Probably too low; see footnote 14.

TABLE 22.—*Correlation between indices of abundance and of fishing intensity for six principal species in Green Bay, 1929–43 and 1929–49*

Species	1929–43		1929–49	
	r	p	r	p
Lake trout	−0.553	$0.05>p>0.02$	−0.316	$p>0.10$
Whitefish	0.819	$0.001>p$	0.761	$0.001>p$
Lake herring	0.310	$p>0.10$	0.270	$p>0.10$
Walleye	0.198	$p>0.10$	0.844	$0.001>p$
Yellow perch	0.152	$p>0.10$	0.184	$p>0.10$
White and redhorse suckers	0.005	$p>0.10$	−0.464	$0.05>p>0.02$

Over the base period 1929–43 only whitefish exhibited a significant positive correlation between abundance and fishing intensity. The correlation for lake trout was significant but negative, and among the remaining species the values of r, all positive, were far below the level of significance ($r=\pm 0.514$ at $p=0.05$ and $df=13$). The addition to the base period of 6 years' data brought about several changes in the relationship. In 1929–49 the value of r for whitefish continued to be positive at a high level of significance, but the correlation between abundance and fishing intensity for lake trout, although still negative, was no longer significant. At the same time a highly significant positive correlation for the walleye and a significant negative correlation for suckers appeared. In lake herring and yellow perch the values of the coefficient continued to fall short of significance.

Although an abundance of fish normally would be expected to stimulate fishing operations[15] and a scarcity to depress them, those studies that have been made of the relation between availability and fishing pressure for individual species have failed to reveal a consistent relation between the two (Van Oosten, Hile, and Jobes 1946; Hile 1949; Hile, Eschmeyer, and Lunger 1951 a and 1951 b). Even where the data have favored the assumption of a cause-and-effect relationship, the correlation has at times been negative. In State of Michigan waters of Lake Superior, for example, the evidence indicates that fishermen increased fishing pressure as the abundance of lake trout declined in order to maintain production at an economically satisfactory level (Hile, Eschmeyer, and Lunger 1951b). In shallow-water fisheries where several species are usually taken together the situation becomes extremely complicated, for it is the total catch of a number of species that determines the financial returns to the fishermen. Our understanding of the economic, biological, and other factors that may influence fluctuations of fishing intensity does not justify a detailed consideration of the problem at this time. The remainder of this section will be restricted, therefore, to comments on certain relationships between abundance and fishing intensity in northern Green Bay for which satisfactory explanations can be advanced.

The fluctuations in the intensity of the fishery for lake trout in the Michigan waters of Green Bay were treated by Hile, Eschmeyer, and Lunger (1951a) who explained the negative correlation between fishing pressure and the abundance of lake trout on the basis of the following points: Lake trout and whitefish are commonly taken together in large-mesh gill nets, with the whitefish normally making up the bulk of the catch; the fishing intensity for whitefish has been correlated closely with the availability of that species and the fishing pressure on lake trout accordingly has tended to fluctuate with the availability of whitefish; the abundance indices of lake trout and whitefish have been correlated negatively, however, and as a result a negative correlation has existed between abundance and fishing intensity for lake trout. Those authors published detailed statistical data in support of their conclusions.

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[15] Excessively high abundance can lead to a glutting of the market with an accompanying collapse of prices and thus depress fishing intensity. Severe market gluts are not common with most Great Lakes species, and when they do occur they usually are so short-termed as to have no great effect on the total annual fishing intensity.

An analogous explanation is believed to hold for the negative correlation between abundance and intensity of the fishery for white and redhorse suckers in 1929–49, with the walleye as the "principal associated species" responsible for the high level of fishing at a time of low abundance of suckers. The 1929–43 data do not indicate a significant correlation between abundance and fishing intensity for either species. (The fluctuations of intensity for walleyes and suckers, however, were positively correlated at a highly significant level—value of $r=0.737$ for the 15 years.) The rise in abundance of walleyes to the unprecedentedly high level of 1947–49 changed the situation for that fish. Walleyes which normally had been taken only incidentally became the primary object of extensive operations. The simultaneous sharp rise of abundance and of fishing intensity increased the correlation coefficient from 0.198 in 1929–43 to 0.844 in 1929–49. Part of the increased fishing for walleyes resulted also in the capture of suckers.[16] Consequently, the intensity of the fishing for suckers rose considerably. Since the level of availability of suckers was low (the abundance indices for suckers in 1947–49 were all below the minimum for 1929–46) a negative correlation between abundance and fishing intensity resulted.

THE PROBLEM OF ECONOMICALLY SOUND REGULATION OF THE FISHERIES

From the preceding discussion it can be seen that the increase which carried the commercial production in Green Bay from the 1929–49 minimum of 1,379,000 pounds in 1944 to nearly 8 million pounds in 1948 and 1949 was largely the result of the exceptionally high abundance of whitefish, lake herring, and walleyes and of greatly increased fishing pressure. This pressure, no doubt, was directed primarily toward the capture of the highly abundant species but those below average abundance (lake trout and suckers) felt its effects. The recovery of the smelt population from the 1943 epidemic also contributed substantially to the heightened production in the late years of the 1929–49 period.

At the end of 1949 the fishing industry of northern Green Bay had enjoyed three consecutive years of production far above the catch in any of the preceding 18 years. During the years of high productivity the market was generally strong and prices, aside from normal seasonal fluctuations, were good. Yet, for all this prosperity, a troublesome situation has developed and, as explained earlier, the groundwork has been laid for possible disaster in the years ahead. The industry may yet pay dearly for these few years of good fishing.

The present difficult situation will become critical at such time as the abundance of fish returns to a more nearly normal level. As was mentioned earlier, numbers of fishermen have moved into Green Bay from other areas. Much of the increase in fishing intensity recorded in the preceding section can be attributed to their activities. Although this increased fishing was desirable in that it made possible the cropping and use of an unusually plentiful supply of fish, the congestion on the grounds and the competition between the newcomers and local fishermen led to some strained relations even when all were making good catches. These relations surely will deteriorate further at such time as the abundance of fish decreases to the point where the available stocks are insufficient to provide profitable fishing for all commercial operators in the area. To be sure, congestion may be relieved somewhat by the return of some of the "migrant" fishermen to their former ports or by their transfer to yet other grounds outside Green Bay; [17] nevertheless, fishing intensity out of proportion to the supply is anticipated. The situation in Green Bay is complicated further by the activities of sportsmen and resort owners who have a strong interest in the sport fishery, especially for walleyes.

The quality of fishing that accompanies fishing intensity of a high level and stocks of only normal abundance will provide a painful contrast with conditions of the past few years, and a loud clamor for protection of the fishery resource is certain to arise. Unless sound judgment prevails, numerous restrictive measures highly detrimental to the industry are almost certain to be enacted. We had a foretaste of this with the introduction of a bill during the 1950–51 session of the Michigan State Legislature to regulate commercial fishing in Delta County (the greater part of the State of Michigan waters of Green Bay lies within its boundaries). Introduced for the stated purpose of protecting the walleye and barely failing of passage, this proposed legislation contained a series of restrictive provisions that would have crippled the industry sadly. Staff members of the Great Lakes Fishery Investigations, when asked to offer an opinion, opposed this legislation on the grounds that it would deprive the community unnecessarily of valuable production and impose severe hardships on commercial operators. Opposition to this measure was not against the principle of a rational control over fishing intensity in a heavily exploited area, but rather against the means proposed for bringing about that control.

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[16] It must be stressed here that fishing intensity is estimated separately for each species. Nets lifted by a fisherman on a particular day are charged against a species only if some quantity of that species is taken.

[17] At the time of preparation of this paper (summer of 1951) we received reports that some fishermen had left Green Bay.

Realistic consideration of the means whereby we can best achieve the goal of a productive and economically sound fishery in the Great Lakes is badly needed. That a fishery, to be of maximum benefit to the community, should be productive would appear axiomatic. Mere abundance of fish, no matter how high it may be, is of no value. It is not the fish that are in the water but the fish that are taken out of the water that provide food and revenue. Yet this axiom often has been disregarded. For the "protection" of fish, productive grounds have been closed, unsound size limits established, species placed on the "game fish" list, and other regulations imposed that serve principally to limit production and create unused stocks.

It may be held axiomatic further that an economically sound fishery not only must show a good level of production with a high dollar value but also must provide the average operator a reasonably good chance for adequate financial returns on his investment and labor. To a large extent the protective regulations in effect in the United States waters of the Great Lakes—size limits that prohibit the capture and sale of fish of a size at which they are plentiful and in demand, closed seasons that forbid operations at a time when fish are easiest to take, closure of grounds to all commercial fishing or the limitation of certain gears to the less productive areas or depths, structural specifications on gears that reduce their effectiveness . . .—limit the income of fishermen by forcing on them inefficient methods of production. The resulting increase in production costs narrows the margin of profit on the one hand and raises the price to the consumer on the other.

It lies outside the scope of this paper to inquire into the actual protective value of the many restrictions on fishing in the Great Lakes or into the soundness of the speculation and theory on which they are based. We are largely without facts to form a judgment. Some may have averted disaster in certain fisheries, others may have had no significant effect either on the stocks or on the conduct of fishing, and still others have, no doubt, been detrimental. A few, such as certain closures of productive areas for the alleged protection of sport fisheries, are indefensible. Although the extent and nature of protection needed and the degree to which present regulations have provided that protection may be debatable, these restrictions unquestionably have served to reduce fishing pressure. The point at issue is the economic expediency of reducing fishing pressure by reducing efficiency of operation.

If the productive capacity of an area is limited, it follows that regulation of fishing pressure may be essential to the economic welfare of the fishery. As the number of units of gear increases, the share available for each unit becomes smaller, and the catch per unit of effort declines—in short, fishing becomes poor. The common remedy for such a situation is to impose restrictions that lessen efficiency of operation and aggravate economic distress by reducing further the catch per unit of effort, and thus add to the cost of production. Fishing pressure may be reduced as some operators are forced out of business or transfer their activities to other grounds, but the control comes from economic hardship, not rational management.

A sounder approach would appear to lie in limiting the units of gear to a number that would assure opportunity for profitable returns per unit of fishing effort. Restricting the number of nets per fisherman or per boat to accomplish this would be of limited value, since with the number of fishermen remaining the same, the share available to each would be unchanged. More effective would be the gradual reduction in the number of licenses (through the retirement of licenses not renewed) until the point is reached at which a reasonably enterprising fisherman can be assured of as great economic stability as is possible in the business he follows. The most modern and efficient methods of capture could be employed and restrictions relaxed, with a resulting decrease in the cost of production and a more dependable profit margin. Without control over the number of licenses issued we can look forward to further legally imposed inefficiency of operation and a continuation of economic instability.

The preceding paragraphs offer a most sketchy treatment of a highly intricate problem; however, the purpose of this discussion is not to undertake a critical analysis of problems of regulation, but merely to point out that economic as well as biological considerations must enter into the framing of a sound program for the utilization of the fishery resources.[18]

SUMMARY

In 1885, the first year for which we have production statistics for the commercial fisheries of the State of Michigan waters of Green Bay, lake herring made up 972,000 pounds, or 39.7 percent, of the total catch of 2,449,000 pounds. Other important species taken were whitefish (31.0 percent), lake trout (16.5 percent), and sturgeon (5.3 percent).

The dominance of lake herring in the catch was much stronger in 1891–1908, the next period for which there are production records. During that period lake herring contributed from 71.6 percent (1905) to 90.6 percent (1899) of the catch in the individual years and had an average take of 5,841,000 pounds or 82.4 percent of the average annual total of 7,085,000 pounds for all species. The mean annual catch and the percentage contribution to the total 1891–1908 production for other important species were: Suckers—398,000 pounds, 5.6 percent; lake trout—213,000 pounds, 3.0 percent; walleyes—197,000 pounds, 2.8 percent; whitefish—159,000 pounds, 2.3 percent; yellow perch—157,000 pounds, 2.2 percent. Despite certain irregularities and possibly some cyclic fluctuations the trends of production in 1891–1908 were decidedly upward for all leading species except walleyes (which were taken in greater quantities in the early than in the late years of the period). The total output (all species) rose from 2.1 million pounds in 1891 to 3.8 million pounds in 1893, dropped to 2.5 million pounds in 1894, and then started on an upward trend that culminated in a take of 10.6 million pounds in 1899. From this high value the catch fell to 6.2 million pounds in 1901, rose (with an irregularity in 1903) to 10.3 million pounds in 1904, dropped suddenly to 7.4 million pounds in 1905, and finally entered on a period of increase that led to the 18-year maximum—in fact, the all-time recorded high—of 13.7 million pounds in 1908. The fluctuations in total yield followed closely those of the dominant lake herring.

Records of production in State of Michigan waters of Green Bay are lacking for 1909–28. When the tabulation of these statistics was resumed in 1929 the species composition of the stock and the level of take had changed markedly. The mean annual yields of the principal species in 1929–49 and their percentage contributions to average annual total of 3,582,000 pounds were: Lake herring—1,070,000 pounds, 29.9 percent; whitefish—714,000 pounds, 19.9 percent; white and redhorse suckers—699,000 pounds, 19.5 percent; smelt (an introduced species)—624,000 pounds, 17.4 percent; yellow perch—150,000 pounds, 4.2 percent; walleyes—133,000 pounds, 3.7 percent; lake trout—126,000 pounds, 3.5 percent.

The 1929–49 fluctuations in production were large for all principal species and tended to be cyclic in some. The ranges in the annual take were: Lake herring—160,000 to 2,668,000 pounds; whitefish—90,000 to 3,066,000 pounds; smelt—nil (no reported commercial catch of this introduced species before 1931) to 2,976,000 pounds; white and redhorse suckers—393,000 to 1,181,000 pounds; yellow perch—49,000 to 361,000 pounds; walleyes—16,000 to 1,063,000 pounds; lake trout—11,000 to 248,000 pounds. These wide fluctuations together with differences in their timing from species to species led to dominance of the total catch first by one variety and then by another. Because of tendencies toward periodicity, dominance by whitefish, lake herring, and smelt lasted 2 to 4 years (lake herring once held first rank for only 1 year). White and redhorse suckers which exhibited little tendency toward periodic fluctuations were dominant three times but never in consecutive years.

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[18] Higgins (1938) pointed out certain economic problems in the management of marine fisheries. Nesbit (1943) discussed the question of control of fishing pressure through limitation of the number of licenses. Taylor, et al. (1951) made an exhaustive analysis of the economics of fisheries.

The total production (all species) stood at 2.3 million pounds in 1929, rose to 2.9 million pounds in 1931, dropped to 1.4 million pounds in 1933, and then increased to 4 million pounds in 1938. The take continued to exceed 4 million pounds in 2 of the next 3 years (it was only 2.7 million pounds in 1939) but 1942 saw the start of a decline that carried the yield to the 21-year minimum of 1.4 million (1,379,000) pounds in 1944. Production increased rapidly during the next 4 years, reaching the 21-year peak of 7.9 million pounds in 1948. The catch was only slightly below this figure in 1949 (7.8 million pounds). The sharp rise to high levels of production in recent years can be traced largely to phenomenal increases in the take of whitefish, lake herring, and walleyes. Production attained the all-time recorded high for whitefish in 1948 and for walleyes in 1949. The catch of lake herring reached the 21-year maximum in 1948, but still was far below the output for certain years in 1891–1908. Also contributing to the increase was the recovery of the smelt stock from the disastrous 1943 mortality; the commercial take of this species increased from less than 500 pounds in 1944 to 1,050,000 pounds in 1949.

The average annual production of 3,582,000 pounds for all species combined in 1929–49 was 3,503,000 pounds or 49.4 percent less than the 1891–1908 mean of 7,085,000 pounds. Decline in the take of lake herring alone (from 5,841,000 pounds in 1891–1908 to 1,070,000 pounds in 1929–49—a drop of 4,771,000 pounds) more than accounted for the difference. For species other than the lake herring the combined average output increased from 1,244,000 pounds in 1891–1908 to 2,512,000 pounds in 1929–49—a rise of 1,268,000 pounds or 102.9 percent. Comparisons of 1891–1908 and 1929–49 production figures throw doubt on the validity of the commonly held belief that most or all major declines in the production of individual species have been the result of overfishing. If we hold, for example, that the huge drop in the average annual catch of lake herring was caused by overexploitation, we are sorely pressed to account for the increase in the output of whitefish, a more valuable species always in high demand, from an annual mean of 159,000 pounds in 1891–1908 to 714,000 pounds in 1929–49. The suggestion is offered that the principal effects of fishing may lie in the disturbance of ecological relationships among species, and that fishing pressure on commercially exploited varieties may have operated so much to the advantage of the smaller, noncommercial species that the latter now make up an increased percentage of the total biological production of fish.

Statistics on distribution of the catch by month and by quarter revealed pronounced differences among the principal species with respect to seasonal trends. Data on the catch by gear demonstrated that all species were taken in quantity by more than one type of gear and that the catches of most gears are made up of several species. The principal gears are gill nets (of three groupings with respect to mesh size), pound nets, shallow trap nets, and fyke and hoop nets.

The fluctuations of abundance (as estimated from the records of catch per unit fishing effort) were considerable for all principal species. Least variable were the abundance indices of yellow perch and white and redhorse suckers. The abundance of lake trout could have been described as moderately steady were it not for the tremendous decline after 1943 (believed to have been caused by the sea lamprey). The most extensive fluctuations in abundance occurred in the whitefish, lake herring, and walleyes. The abundance indices of these species were particularly high during the last 3 (whitefish, walleyes) or 5 (herring) years of the period. Maximum levels attained (indices expressed as percentages of the average 1929–43 abundance) were: Whitefish—275 in 1947; lake herring—367 in 1946; walleyes—344 in 1949 (this last figure may be an overestimate, see p. 22). The available evidence indicates that the attainment of these high values was made possible by the phenomenal strength of the 1943 year class of all three species. The late development of the smelt fishery and the disruption occasioned by the 1943 mortality have prevented the establishment of suitable norms for the estimation of fluctuations in the abundance of that species.

Of the 15 coefficients of correlation that could be computed between abundance percentages among the 6 principal species, 7 were significant (5 were negative and 2 were positive). Additional significant coefficients were obtained when time lags of 1 to 3 years were established. With the whitefish and walleyes a significant negative correlation for 1929–38 was followed by a highly significant positive correlation in 1939–47. Only a greatly expanded knowledge of the natural history of Green Bay fish can explain these interrelationships.

Correlations between annual fluctuations in abundance and production indicated that production would have served as a reasonably dependable indicator of the major changes of availability in 1929–49 for whitefish, lake herring, walleyes, yellow perch, and suckers, but would have been highly misleading for lake trout.

The abundance of fish and the intensity of fishing exhibited highly significant positive correlation for whitefish in the 1929–43 base period and in 1929–49, and for walleyes in 1929–49. Our knowledge of the fishery prompts us to view these correlations as reflecting a true cause-and-effect relation. The remaining coefficients fell short of significance or had significant negative values (lake trout in 1929–43; white and redhorse suckers in 1929–49). These negative coefficients were explained as the result of heavy fishing for whitefish and walleyes in which lake trout and suckers were taken as incidental parts of the catch during periods of low abundance of the latter two species.

An outstanding feature of the data on fishing intensity was the extremely great pressure directed against most species during the last 2 or 3 years of the 1929–49 period. The maximum levels (indices give as percentages of the average 1929–43 intensity) attained for the different varieties in recent years were: Lake trout—253 in 1948; whitefish—407 in 1949; lake herring—195 in 1948; walleyes—615 in 1949 (possibly an underestimate); yellow perch—77 in 1949; white and redhorse suckers—194 in 1949. Higher levels of fishing intensity were reached in earlier years by only two species: Lake herring—220 in 1938; yellow perch—190 in 1938.

The upswing of production that carried the annual take from the 21-year low of 1.4 million pounds in 1944 to nearly 8 million pounds in 1948 and 1949 was made possible to a large degree by the phenomenal increase in the abundance of whitefish, lake herring, and walleyes and by an enormous expansion of fishing activity (much of it to be traced to fishermen who moved in from other areas). Although the cropping of this large supply of fish was desirable a dangerous situation has been created. At such time as the abundance of fish returns to a more nearly normal level the available supply may be inadequate to support profitable operations for all the fishermen in the bay. Not only will the fishermen experience financial difficulties, but there is a real threat of the enactment of "protective" legislation that could all but destroy the fishing industry.

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SUPPLEMENT—THE FISHERY OF GREEN BAY IN 1950

After completion of the main body of the present paper on fluctuations in fish populations and take in the Green Bay fisheries through 1949, statistics became available for 1950, and are presented here. The following comments are concerned principally with comparisons of 1949 and 1950 levels of yield, abundance, and fishing intensity for the principal species (table 23). Records of the catch per lift on which estimates of abundance were based are given in table 24 and detailed figures on production are included in table 25. Understanding of these tables will be furthered by references to earlier tables in the text giving corresponding data for 1929–49.

Lake trout: A decline in abundance from 45 in 1949 to 23 (the 1929–50 low) in 1950 and a drop in fishing intensity from 207 to 40 combined to reduce the take from 149,000 pounds (102 percent of the 1929–43 mean) in 1949 to 15,000 pounds (10 percent) in 1950. With the exception of the 11,000-pound catch in 1946, the 1950 take was a record low.

Whitefish: Abundance changed little from 1949 (158) to 1950 (156) but fishing intensity dropped from 407 to 272. The take accordingly fell more than three-quarters of a million pounds—from 2,263,000 pounds to 1,494,000 pounds. Even so, the 1950 yield exceeded 3½ times the 1929–43 average.

TABLE 23.—*Levels of production, abundance, and fishing intensity for the principal species in Green Bay, 1949 and 1950*

[In thousands of pounds; index figures as percentages of the 1929–43 mean]

Species	Production		Production index		Abundance index		Fishing intensity index	
	1949	1950	1949	1950	1949	1950	1949	1950
Lake trout	149	15	102	10	45	23	207	40
Whitefish	2,263	1,494	543	358	158	156	407	272
Lake herring	2,230	3,249	312	455	228	222	145	218
Walleyes	1,063	1,294	2,093	2,547	344	([1])	615	([1])
Yellow perch	65	107	37	61	49	52	77	119
White and redhorse suckers	878	729	120	99	61	63	194	155
Smelt	1,050	1,624	144	222	------	------	------	------
All species	7,782	8,578	256	282	------	------	------	------

[1] Estimates not attempted for 1950; abundance index in 1949 probably too high and intensity index too low; see text, p. 22.

TABLE 24.—*Catch, in pounds, of principal species of fish per unit of effort in Green Bay, by gear, 1950*

[Figures, except for smelt, are based on annual totals of production and gear lifted]

Species	Gill nets [1]			Pound nets [4]	Shallow trap nets [4]	Fyke and hoop nets [4]
	Bait [2]	Small-mesh [3]	Large-mesh [3]			
Lake trout	--------	--------	23	2	--------	--------
Whitefish	--------	--------	167	88	--------	--------
Lake herring	--------	2,081	--------	187	--------	--------
Walleyes	--------	--------	--------	21	74	56
Yellow perch	--------	133	--------	--------	6	23
White and redhorse suckers	--------	--------	170	18	53	48
Smelt:						
January	28	--------	--------	41	--------	--------
February	27	--------	--------	171	--------	--------
March	21	--------	--------	286	--------	--------
April	73	--------	--------	450	--------	--------

[1] Mesh sizes, extension measure: bait nets, mostly 1½–1⅝ inches; small-mesh nets, 2¼–2¾ inches; large-mesh nets, 4½ inches and larger.
[2] Unit of effort: lift of 1,000 linear feet.
[3] Unit of effort: lift of 10,000 linear feet.
[4] Unit of effort: lift of one net.

Lake herring: The rise of more than a million pounds in the output of lake herring, from 2,230,000 pounds (312 percent of the 15-year average) in 1949 to 3,249,000 pounds (455 percent) in 1950 can be traced entirely to an increase in fishing intensity from an index value of 145 to one of 218. The availability of lake herring declined (from 228 to 222) but was extremely high in both years.

Walleye: The production which amounted to 1,063,000 pounds, or 2,093 percent of the 1929–43 mean, in 1949 was increased further to the all-time recorded high of 1,294,000 pounds, or 2,547 percent, in 1950.

We are, unfortunately, without basis for a good estimate of the relative importance of the abundance of walleyes and of fishing intensity in this record output. The difficulty in estimating abundance and fishing intensity originates in uncertainty as to whether the catch per lift of shallow trap nets in the most recent years is in fact comparable with the "normal" established for that gear for the base period 1929–43. When discussing the 1929–49 fluctuations in abundance, we called attention to the fact that during the later years of that period, particularly 1947–49, the catch per lift was relatively much more above the 15-year mean in trap nets than in pound nets or fyke nets, the other two gears employed in the estimation of abundance.[19] Much of the relatively greater success of the trap nets, it was explained, probably resulted from the introduction of larger nets capable of taking more walleyes per lift at a given population level than were taken by the gear formerly employed. Any increases in the catch per net that resulted from change of gear rather than from increased abundance, of course, contributed to an overestimate of the index of abundance and an underestimate of the index of fishing intensity.

The discrepancies between the data for trap nets and those for pound nets and fyke nets that were troublesome in the 1947–49 statistics became excessive in 1950, as is seen from the following tabulation:

	Catch per lift (pounds)		*1950 catch as percentage of average*
	1929–43	*1950*	
Pound nets	19	21	111
Shallow trap nets	8	74	925
Fyke nets	32	56	175

Although the discrepancies indicated above are so large as to make the computation of general indices of abundance and fishing intensity undesirable, the original data do provide some useful information. There can be little doubt, for example, that in 1950 the abundance of walleyes continued to be substantially above the 1929–43 average. The lowest estimate for a single gear was 111 percent (pound nets) and the other gear for which we have no reason to suspect biased records (fyke nets) yielded the higher figure of 175. Furthermore, we cannot overlook the possibility that the high figure for trap nets resulted from a heavy concentration of walleyes on the trap-net grounds as well as from the introduction of more efficient nets. Hence, on those fishing grounds the relative abundance may have been in fact at a level higher than that indicated by the data for either pound nets or fyke nets.

The continued high (if not precisely measured) abundance and the enormous yield of walleyes in 1950 are a tribute to the phenomenal strength of the 1943 year class. That group, according to Robert F. Balch,[20] strongly dominated the commercial catch in State of Michigan waters of Green Bay in 1950; furthermore, an early 1951 sample indicated that walleyes hatched in 1943 would form the main support of the 1951 fishing.

Yellow perch: The year 1950 saw an end to the downward trend that had carried the index of abundance from a high of 150 in 1945 to 49 in 1949. The improvement to 52 in 1950 was, of course, small, but it does lend hope that a recovery of the stocks may be under way. The increase in the catch of yellow perch from 65,000 pounds (37 percent of the 1929–43 average) in 1949 to 107,000 pounds (61 percent) in 1950 came principally from the upswing in fishing intensity from an index value of 77 in the former year to one of 119 in the latter.

White and redhorse suckers: With the suckers as with the yellow perch a slight rise in the abundance index (from 61 in 1949 to 63 in 1950) gives us hope that a period of low availability may be nearing its end. Despite the small improvement in abundance the production of suckers fell from 878,000 pounds (120 percent of the 15-year normal) in 1949 to 729,000 pounds (99 percent) in 1950. The decline can be traced to a drop in fishing intensity from 194 to 155.

Smelt: The recovery of production following the mortality of 1943 continued in 1950 when the catch of 1,624,000 pounds (222 percent of the 1929–43 mean) was 574,000 pounds greater than the 1949 yield of 1,050,000 pounds (144 percent). Comparisons of the catch per lift in 1950 (table 24) with those of 1949 (table 17) prove that the increase in the take resulted from an upswing in fishing pressure. With the exception of the equal catches of 28 pounds per 1,000 feet of bait nets in January of both years, the production per unit of fishing effort was consistently higher in 1949 than in the same month and with the same gear in 1950.

Total production: The take of 8,578,000 pounds (282 percent of the 1929—43 average) constituted a new high in the modern period which began with 1929. The principal contributors to the rise from 7,782,000 pounds (256 percent) in the previous year were lake herring, smelt, and walleyes with increases of 1,019,000, 574,000, and 231,000 pounds, respectively. These increases, together with those of yellow perch and of certain minor species, exceeded by 796,000 pounds the decreases in the take of whitefish (769,000 pounds), white and redhorse suckers (149,000 pounds), lake trout (134,000 pounds), and other varieties.

---

[19] Data from large-mesh gill nets, a major gear in the production of walleyes in 1947–50, cannot be used for the estimation of abundance since we have been unable to establish a long-term normal catch per lift. In 1929–46, the production of walleyes by this gear was too small to yield dependable data on the take per unit effort. The annual take averaged only 1,946 pounds over that period, and in 7 of the 18 years the catch was less than 1,000 pounds.

[20] Unpublished manuscript submitted to the Wisconsin Conservation Department.

Pound nets, which took 3,157,000 pounds, or 36.8 percent of the total, were the most productive gear in 1950 (table 25). Next in importance were large-mesh gill nets (1,998,000 pounds, 23.3 percent), small-mesh gill nets (1,996,000 pounds, 23.3 percent), and shallow trap nets (1,330,000 pounds, 15.5 percent). No other method of fishing contributed as much as 1 percent of the total.

The 1950 production of 8,578,000 pounds in Green Bay constituted 70.2 percent of the State of Michigan total of 12,223,000 pounds for Lake Michigan. The corresponding percentage was 65.4 in 1949.

TABLE 25.—*Production of each species of fish in Green Bay, by gear, 1950*

[In pounds]

Species	Gill nets [1]			Pound nets	Shallow trap nets	Fyke and hoop nets	Seines	Hand line and trolling	Total	Percentage
	Bait	Small-mesh	Large-mesh							
Lake trout	----------	5	14, 455	249	----------	----------	----------	----------	14, 709	0. 2
Whitefish	----------	207	1, 007, 323	470, 993	15, 041	----------	----------	----------	1, 493, 564	17. 4
Lake herring	313	1, 893, 512	16, 929	1, 007, 941	330, 456	121	----------	----------	3, 249, 272	37. 9
Walleyes	----------	129	559, 714	99, 110	624, 279	10, 230	----------	51	1, 293, 513	15. 1
Yellow perch	----------	68, 732	285	5, 603	27, 153	4, 759	----------	293	106, 825	1. 2
White and redhorse suckers	----------	1, 948	359, 820	38, 458	321, 748	7, 308	----------	----------	729, 282	8. 5
Smelt	69, 104	8, 922	11, 551	1, 534, 228	----------	----------	----------	----------	1, 623, 805	18. 9
Others [2]	----------	22, 634	27, 446	683	11, 621	1, 901	2, 717	----------	67, 002	. 8
Total	69, 417	1, 996, 089	1, 997, 523	3, 157, 265	1, 330, 298	24, 319	2, 717	344	8, 577, 972	----------
Percentage	0. 8	23. 3	23. 3	36. 8	15. 5	0. 3	[3] 0. 0	[3] 0. 0	----------	----------

[1] Mesh sizes, extension measure: Bait nets, mostly 1½–1⅝ inches; small-mesh nets, 2¼–2¾ inches; large-mesh nets, 4½ inches and larger.

[2] Includes (catches in pounds of all gears combined): Chubs, 21,784; carp, 18,880; longnose suckers, 10,260; northern pike, 8,570; bullheads, 3,908; rock bass, 1,630; round whitefish, 1,373; saugers, 220; sheepshead, 137; burbot, 121; catfish, 103; bowfin, 8; white bass (actually not a commercial species), 8.

[3] Less than 0.05.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

A CONTAGIOUS DISEASE OF SALMON POSSIBLY OF VIRUS ORIGIN

By R. R. Rucker, W. J. Whipple, J. R. Parvin
and C. A. Evans

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A CONTAGIOUS DISEASE OF SALMON, POSSIBLY OF VIRUS ORIGIN

By R. R. Rucker,[1] *Fishery Research Biologist*, W. J. Whipple[1] and J. R. Parvin,[1]
Fish Culturists, and C. A. Evans,[2] *Microbiologist*

OUTBREAK OF DISEASE AT THE LEAVENWORTH STATION, 1951

An outbreak of disease in 1951 among two groups of salmon fingerlings at the U. S. Fish and Wildlife Service station, Leavenworth, Wash., caused extensive losses. One of the affected groups was the blueback, or sockeye, salmon (*Oncorhynchus nerka*), which spends the first 12 to 24 months of its life in lake waters, and most of the next 2 years in salt water. It then returns to fresh water to spawn when about 4 years old. The other group was the landlocked salmon, or kokanee (*O. nerka*). It is of the same species, but differs from the blueback in that it spends its entire life in fresh water.

Transmission experiments indicated that a filtrable agent, presumably a virus, was the cause of this disease. The appearance of the sick fish, the findings at autopsy, and certain other characteristics of this epizootic closely resembled a disease seen previously among kokanee and blueback-salmon fingerlings at the Winthrop, Wash., station. Diet is not discussed, as the diets employed were used successfully at other stations in rearing similar fish.

This disease appears to be a significant problem in practical hatchery management. In addition, it is of interest in the field of comparative pathology in view of the probability that the causative agent is a virus. A noteworthy feature seen in a small number of the infected fish, particularly those that survive for relatively long periods, is a peculiar distortion of body shape comparable to scoliosis and lordosis as manifested in certain human diseases.

Facilities for this study were furnished by the School of Fisheries, University of Washington. Technical assistance of J. M. Alexander and S. W. Watson is gratefully acknowledged.

DISEASE AMONG BLUEBACK-SALMON FINGERLINGS

A group of about 1,400,000 blueback-salmon fingerlings which started feeding at the Leavenworth station on January 5, 1951, had insignificant losses—fewer than 300 daily—for 2½ months. These fish occupied 102 troughs. On about March 20, fish in one of the troughs were observed to have a higher mortality than those in the other troughs. Mortality data for the next 10 days are not available, but it is known that by the end of March about 13,000 fish were left in this trough. They were now approximately 2 inches long and 3 months old. Table 1 shows the number of these that died each day, April 1 to 10. After this date the surviving fish were used for therapeutic studies, and practically all of them eventually died from the disease.

TABLE 1.—*Daily mortality in 13,000 blueback-salmon fingerlings, Leavenworth station, April 1–10, 1951*

Date	Mortality	Date	Mortality
Apr. 1	163	Apr. 8	761
2	185	9	654
3	296	10	900
4	225		
5	270	Total	4,350
6	379	Percentage	33.5
7	517		

A similarly severe mortality occurred in five more troughs. In the six troughs, with a total population in excess of 80,000 fish, the mortality rate during March, April, and the first 3 weeks of May was virtually 100 percent. In contrast, during this same period the mortality rate in the remaining 96 troughs that contained some 1,300,000 fish was approximately 1 percent a month.

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[2] Department of Microbiology, University of Washington Medical School, Seattle, Wash.

These healthy blueback salmon were placed in outside ponds for rearing during the early part of June. They continued in excellent condition throughout the summer and had a very low mortality.

The water temperatures increased during the summer as shown in table 2; but when they began to drop in the fall, the mortality rate again increased slightly among the blueback salmon and the disease reappeared. This was indicated by the mortality of 0.4 percent for the 11-day period ended October 5. This represented a mortality rate more than twice that of the preceding 2 weeks and more than four times the rate during August and the first part of September. There was a progressive increase in daily mortality during the last 9 days prior to planting the fish on October 5.

Table 2.—*Biweekly mortality in salmon fingerlings with average water temperature, Leavenworth station, 1951*

[Original number: 1,400,000 blueback salmon and 788,000 kokanees]

Period ended	Blueback mortality	Kokanee mortality	Average water temperature
	Percent	*Percent*	*° F.*
Feb. 12	0.8		46
26	.7		46
Mar. 12	.6		46
26	1.1		45
Apr. 9	.8		45
23	1.2	3.6	45
May 7	2.4	3.4	45
21	2.5	2.4	44
June 4	.6	5.4	44
18	.2	1.2	46
July 2	.1	10.6	49
16	.2	14.4	56
30	.2	2.7	59
Aug. 13	.1	1.6	59
27	1	1.5	59
Sept. 10	.1	.8	54
24	.2	.5	52
Oct. 5	.4		49
9		1.0	49
Total	11.4	39.6	

Note.—Mortality is based on the percentage of fish alive at the beginning of each biweekly period. Total mortality is therefore not equal to the sum of the biweekly percentage mortalities.

Oct. 5 and Oct. 9 indicate planting dates, not biweekly periods.

The disease among the blueback-salmon fingerlings at the Leavenworth station in 1951 was demonstrated by a number of techniques to be contagious. The 1,400,000 young bluebacks were held in 102 troughs arranged in pairs separated by aisles. The troughs were tended by two workers using alternate aisles. Thus, each worker cared for the fish in the troughs on both sides of alternate aisles as shown in table 3. The pattern in which the disease spread among six troughs cleaned by one worker suggested an infectious disease, probably transmitted by equipment used to clean the troughs. As soon as it was suspected that an infectious agent was present, all cleaning equipment was sterilized between use in individual troughs by dipping it in a disinfectant. A 1:2,000 solution of roccal was used. It is remarkable that the infection was limited to the six troughs, presumably as a result of this precaution.

Table 3.—*Course of the disease through 6 troughs of blueback fingerlings, Leavenworth station, 1951*

[Total of 102 troughs and 1,400,000 fingerlings]

Adjacent pairs of troughs	Worker tending troughs	Order of infection	Date trough was infected
Trough 181	No. 1	No disease	
Trough 182	No. 2	Sixth	May 9
Trough 183	No. 2	Fifth	Apr. 29
Trough 184	No. 1	No disease	
Trough 185	No. 1	do	
Trough 186	No. 2	Third	Apr. 19
Trough 187	No. 2	First	Mar. 20
Trough 188	No. 1	No disease	
Trough 189	No. 1	do	
Trough 190	No. 2	Fourth	Apr. 26
Trough 191	No. 2	Second	Apr. 16
Trough 192	No. 1	No disease	

Appearance of Diseased Fish

A definite diagnosis could not be made either from the appearance of the sick fish or from the findings at autopsy. The findings conformed to a general pattern that might also occur in fish with other diseases.

Diseased fish appeared lethargic and did not react to stimuli, such as moving an object over the trough or jarring the trough. Normal fish would dart about, but sick fish usually did not move. After a few days, the abdomen was slightly bulged. A few fish showed hemorrhagic areas in some of the fins, at the base of paired fins, or in the isthmus; and the gills were pale.

In autopsied fish, the spleen was often light in color; the stomach was distended with a milky fluid, giving the impression of pyloric constriction; the gall bladder was filled with green bile, which in fish is typical of anorexia; the intestine was full of a watery, straw-colored fluid; and the large intestine often was red and apparently inflamed. Fluid expressed from the anus was yellowish and generally tinged with blood. There was some muscular necrosis in the anal region.

Scoliosis developed during May in about 0.1 percent of the original population in the six troughs of diseased fish, and some fish with retracted heads were observed (see fig. 3).

The rest of the blueback fingerlings exhibited no characteristic disease symptoms throughout the summer, but during the first week of September, when water temperatures became progressively colder, diseased fish were again seen. At this time the fish were about 4 inches long and 8 months old. Diseased fish showed a reddened large intestine and a watery, bloody, yellowish discharge from the anus. About half of these had areas of fungus growth, predominately at the base of the pectoral, pelvic, or anal fins. These were the sites where hemorrhagic areas were seen on diseased fish in the spring. Fungus generally indicates debilitation or the presence of necrotic tissue. In September approximately half of the diseased fish exhibited spinal deformities; of these 60 percent had retracted heads, 30 percent scoliosis, and 10 percent lordosis (see fig. 1). Many fish showed no external signs of the disease other than these abnormal body shapes. A number of fish with spinal deformities had a surface growth of fungus, but autopsy of a few fish with scoliosis revealed no internal abnormalities.

Therapeutic Tests

The routine hatchery treatments of 1-hour baths in solutions of 1:4,000 formalin or of 1:100,000 pyridylmercuric acetate failed to influence the mortality rate. Therefore, sulfonamides and antibiotics were used experimentally on the fish that showed evidence of the infection. (See figure 2.)

When the fish in a trough became diseased they were divided into several groups and transferred to other troughs. The therapeutic agents were added to the food. Sulfamerazine, sulfaguanidine, sulfadiazine, and sulfamethazine were each used at the rate of 10 grams to 100 pounds of fish a day. The antibiotics were also added to the food at levels for 100 pounds of fish as follows: Aureomycin 1.5 grams in experiment A and 5 grams in experiment D; terramycin 2.5 grams; chloromycetin 2.5 grams; streptomycin 10 grams; and penicillin 1 million units in experiment C and 10 million units in experiment D.

The cumulative mortalities, shown in figure 2, are expressed as the percentage of the total mortality for each group. There was some difference in the total numbers of fish in the different troughs. At the beginning of an experiment, the number of fish in each trough was necessarily an estimate, and actual counts were made as the fish died. In experiment C, only an estimate is available (5,000 fish per trough) since the experiment was terminated at an early date because the drugs apparently were ineffective, and it was desired to set up another experiment at a higher drug level.

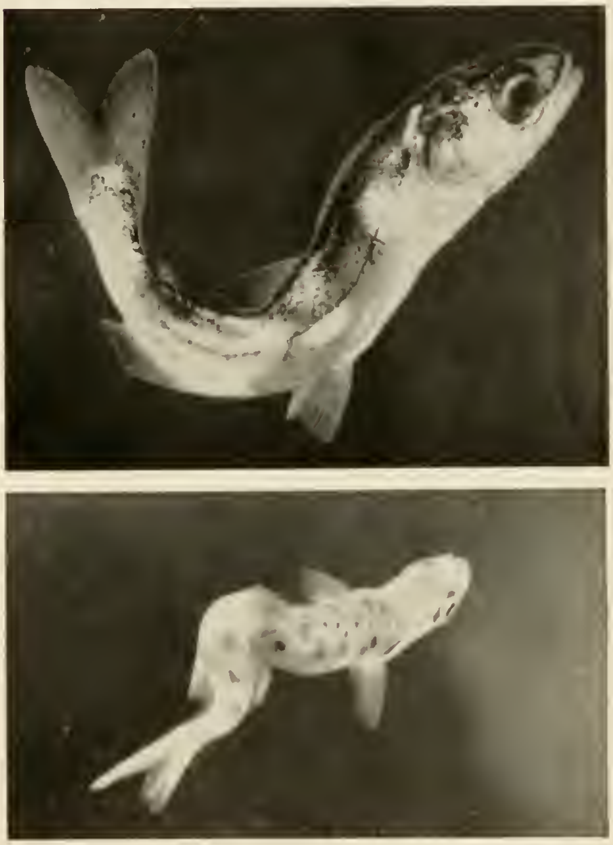

FIGURE 1.—Living blueback-salmon fingerlings from the Leavenworth station, showing lordosis in a 4-inch fish (upper) and scoliosis in a 3-inch fish (lower).

None of the therapeutic agents tested seemed to be of any benefit; the mortalities continued. Practically all fish died in each experiment regardless of the therapeutic agent employed.

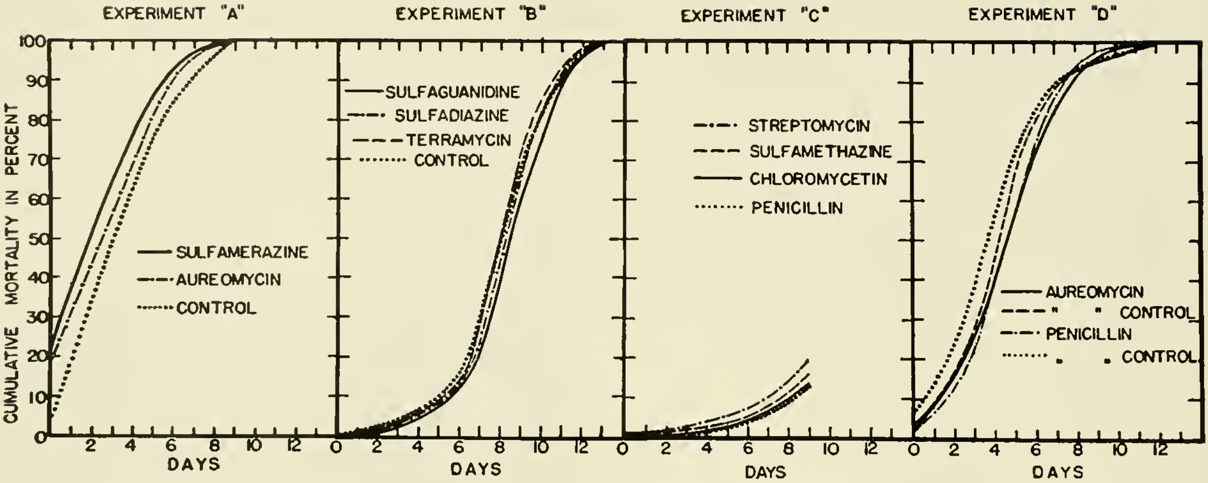

FIGURE 2.—Effect of sulfonamides and antibiotics on diseased blueback-salmon fingerlings at the Leavenworth station, 1951. The number of fish in each trial varied between 2,000 and 5,000 depending on the number of diseased fish available. Experiments A, B, C, and D were run at different times. Fish used in experiment C were transferred on the ninth day to experiment D. Practically all the fish died.

Experimental Transmission

To determine the nature of this disease, healthy blueback-salmon fingerlings were placed among diseased ones. They were obtained from a trough showing negligible mortality, and appeared to be in excellent health. One group of healthy fish was placed in a compartment with diseased fish; a second group was held in a separate compartment at the lower end of the same trough. Both groups showed signs of the disease after 12 days. Fish in the trough from which the healthy fish were taken remained well. Healthy fish placed in another trough of healthy fish, as a control, did not develop the disease. Silver-salmon fingerlings (*O. kisutch*) and cutthroat-trout fingerlings (*Salmo clarki clarki*) did not contract the disease when exposed in a similar manner to diseased fish.

No parasites could be demonstrated in diseased fish by the examination of stained tissue or by phase microscopy of fresh material. Similarly, attempts to isolate bacteria from diseased tissue yielded sterile cultures or organisms that were regarded as contaminants.

Broth and solid and semisolid media incubated at various temperatures and under both aerobic and anaerobic conditions were used. The composition of the media varied from rich media as brain-heart infusion (Difco), through peptones of various strengths, to dilute extracts of fish. Some media were enriched by the addition of ascitic fluid, yeast infusion, or fish extracts.

In two experiments, Seitz filtrates of suspensions of tissue from fish showing typical signs of the disease failed to infect a total of 20 inoculated fish. Control fish inoculated with unfiltered material died. However, bacteria capable of infecting injected fish were recovered from the controls. It is probable that the infecting virus was present, together with bacteria, in the unfiltered inoculum since in other similar experiments, when a coarser filter was used (7-pound-test Mandler filter), the filtrate was infectious and tests for bacteria were negative. The experiments are therefore not conclusive, but are interpreted as indicating that the infectious agent probably will not pass a Seitz filter.

DISEASE AMONG KOKANEE FINGERLINGS

While this disease was present among the blueback-salmon fingerlings, a group of 788,000 kokanee fingerlings also became affected at the Leavenworth station in 1951. As shown in table 2, the mortality amounted to about 40 percent of the population.

Evidence of the disease was first observed in one trough on May 18. The losses increased very rapidly during the next few days, and the fish in this trough were destroyed to prevent spread of the infection. By May 27, fish in another trough showed signs of the disease. It appeared that the disease was kept somewhat under control after this time by sanitary measures and the fish were put in outside ponds on July 18. The disease became less prevalent in midsummer but increased in severity in the fall. It is possible that the decreased mortality in summer was related to the increase in water temperatures. Table 2 lists the water temperatures (range, 44° to 59° F.) for the period February 12 to October 9, and gives the biweekly mortality data. The daily mortality rate showed a definite increase during the latter part of the last 2-week period, although the table shows only the biweekly mortality. The characteristics of the diseased fish indicated that the disease was definitely approaching an epizootic stage when they were planted, having undergone a 39.6-percent mortality attributed to this disease.

Appearance of Diseased Fish

The kokanees were approximately 3 months old and about 1 inch long when the epidemic began in May. As a group, the larger fish appeared to suffer greater mortality than those of average or small size. Signs of the disease in the kokanees were similar to those in the bluebacks. The fish were apathetic; their gills were pale; some showed a flush of red at the base of the fins or on the operculum; and some exhibited popeye (exophthalmos). The spleen was often pale; hemorrhagic areas on the air bladder or necrotic areas in the musculature near the vent or dorsal area were found in some; and the gastrointestinal tract contained a watery fluid. The diseased fish appeared black from above while normal fingerlings were olive green.

At the end of the season spinal curvatures were not as frequent in the 2-inch kokanees as they were in the 4-inch bluebacks previously mentioned. About 0.1 percent of the total population of kokanees developed scoliosis, mainly during the period July to October. In the fall, when the mortality rate increased, fish with retracted heads became common. In figure 3, the characteristic posture is shown. The lateral view shows how the head was retracted. The dorsoventral distance was increased remarkably just posterior to the orbital area.

Experimental Transmission

The infectious nature of the disease among the kokanees was demonstrated in the following experiment. Twenty thousand kokanees from the last trough to show signs of the disease were divided equally between two adjacent troughs. One group served as the control. For a period of 2 weeks the other group was treated every other day for 1 hour with 1:100,000 pyridylmercuric acetate. There was no diminution of the mortality rate.

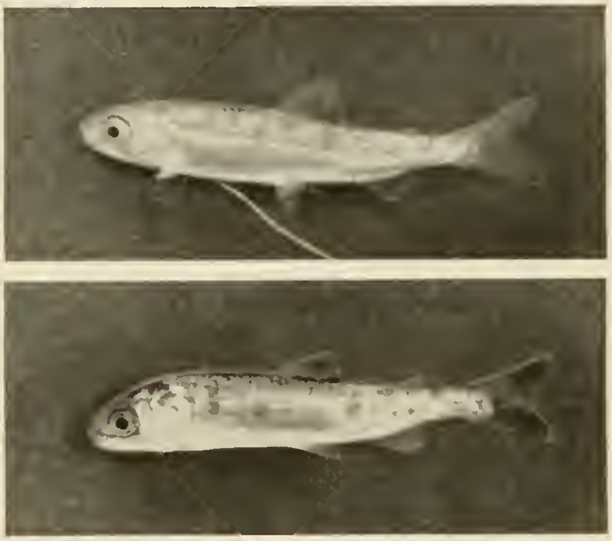

Figure 3.—Normal (upper) and diseased (lower) 2-inch living kokanee fingerlings from the Leavenworth station. The diseased fish shows the retracted head.

In another experiment, two adjacent troughs were each stocked with 10,000 healthy kokanees. One trough was cleaned with equipment also used on the troughs containing diseased kokanees, the other with separate equipment disinfected with roccal. About 12 days after initiation of the experiment an increased mortality was noted among the fish in the trough cleaned with contaminated equipment. During the next 48 hours, an additional large number of fish became sick, showing characteristics of the disease. The disease did not appear in the second group, and the experiment was terminated at this time. The infectious nature of the disease affecting the kokanees was thus shown to be similar to that affecting the blueback-salmon fingerlings.

As in the blueback salmon, a search for parasites that could be responsible for the disease was unsuccessful. Similarly bacteriological studies failed to provide an explanation for it. To test for a filtrable infectious agent, a suspension was prepared by blending one group of moribund kokanees with Ringer's solution; a second suspension was prepared from a group of five fish with scoliosis and five with lordosis by grinding them in Ringer's solution with mortar and pestle. Both suspensions were centrifuged.

A portion of each suspension was passed through a 7-pound-test Mandler filter that retained bacteria. Portions of both filtered and unfiltered material were heated at 80° C. for 15 minutes. Each of the four preparations was injected into a group of 20 2- to 3-inch healthy kokanee fingerlings. Ten of each group were injected intramuscularly with 0.1 milliliter and 10 intraperitoneally with the same amount.

Ninety-five percent of the fish injected with the unfiltered and unheated material from both original suspensions died within a week (table 4) with evidence of inflammation and necrosis of the muscle in the area of the injection or inflammation throughout the body cavity and viscera. Cultures from these fish indicated the presence of miscellaneous bacteria. Death was probably the result of infection by bacterial contaminants, and not related to the disease in the hatchery. No fish died among those injected with the heated material.

TABLE 4.—*Mortality of healthy kokanee fingerlings injected with fractions of diseased kokanees Leavenworth station, 1951*

[IP—group injected intraperitoneally; IM—group injected intramuscularly; each group comprised 10 fish]

Date	Deaths among fish injected Sept. 28, 1951, with suspension from moribund kokanees								Deaths among fish injected Sept. 30, 1951, with suspension from kokanees with scoliosis and lordosis							
	Unfiltered				Mandler filtrate				Unfiltered				Mandler filtrate			
	Unheated		Heated		Unheated		Heated		Unheated		Heated		Unheated		Heated	
	IP	IM	IP	IM	IP	IM	IP	IM	IP	IM	IP	IM	IP	IM	IP	IM
Sept. 30	1															
Oct. 1																
2	2	7														
3	4	2			1					2						
4	1					1			1	4						
5	1					1			3	2						
6	1								4	2						
7													3	3		
8					2	1										
9						2								2		
10													2	1		
11																
12						(1)										
13						1							1			
16									1							
23						1										
Total	10	9			3	7			9	10			6	6		
Combined mortality, Nov. 30 (percent)	95		0		50		0		95		0		60		0	

[1] One missing.

Fifty percent of the fish that were injected with the Mandler filtrate of the suspension of moribund fish died in a period of 1 month. They developed petechiae at the base of paired fins, on the isthmus, or on the side of the body. The viscera were inflamed, and often the inoculation site showed inflammation with some necrosis in the muscle. Cultures of kidney and muscle on agar yielded colonies of a variety of bacteria on about half the plates, presumably contaminants or secondary invaders. The other plates remained negative.

Sixty percent of the fish died that were injected with the Mandler filtrate of the suspension from kokanees affected with scoliosis and lordosis. They also showed areas of inflammation on the body surface, at the base of the fins, on the isthmus, on the viscera, fat, and especially on the intestine. Bacteria were not always recovered from the kidney and muscle cultures from dead fish, but usually these cultures yielded miscellaneous forms, presumably contaminants or secondary invaders. Thirty-four days after inoculation, one intramuscularly inoculated fish showed a slight reddening in the dorsal-fin area and a tendency toward lordosis. Photographs of this fish demonstrate the progressive nature of the disease (fig. 4). One intraperitoneally inoculated fish showed the first signs of developing scoliosis 42 days after injection. This fish was photographed to show the progressive development of scoliosis (fig. 5). Observations on this experiment were terminated November 30, 1951, 5 weeks after the last mortality occurred.

OUTBREAK OF DISEASE AT THE WINTHROP STATION, 1949–51

BLUEBACK BROOD OF 1950

At the time of the outbreak of disease at the Leavenworth station in the spring of 1951, there was a similar occurrence of disease at the Winthrop station. Blueback-salmon eggs taken at Winthrop in the fall of 1950 were hatched both at the Winthrop and the Leavenworth stations. Fingerlings from the eggs retained at the Winthrop station were raised without significant loss up to the time of their release on April 20, 1951. A group of 69,000 fingerlings from the same group of eggs, hatched and raised at the Leavenworth station to a size of about 1½ inches, was transferred to the Winthrop station on March 8, 1951. Mortality among this group of fish was above normal in April, and most of the fish were lost from disease during May when they were about 2½ inches long and 5 months old. The disease began in one trough, approximately 7 days later was found in two more troughs, and then became general.

The disease was characterized by the rapidity with which it spread and by the death of many fish without apparent gross abnormalities. Many fish had hemorrhagic areas on or at the base of the fins and on the isthmus. Some had fungus growing on the peduncle, around the dorsal fin, or at the base of the pectoral fins. The gills were a normal red, but the spleen often appeared pink. Moribund fish showing external lesions had normal-appearing spleens. No solid material was found in the stomach which, in common with the intestine, contained a clear to yellowish fluid. There was no response to sulfadiazine or aureomycin therapy. Scoliosis developed in about 5 percent of the diseased fish.

BLUEBACK BROOD OF 1948

Losses among the blueback-salmon fingerlings and yearlings at the Winthrop station over the previous several years had on occasion been rather high. Necrosis of the kidneys was common and bacteriologic studies indicated that a short Gram-positive rod of the kind described by Earp (1950) was the etiologic agent. During the winter of 1949–50, sulfadiazine therapy was employed in an attempt to reduce the losses among the blueback-salmon fingerlings (Winthrop brood of 1948). Rucker, et al. (1951) working with a group of these fish found that sulfadiazine controlled the kidney infection among the population at the hatchery, but the mortality rate continued high—about 10 percent a month of 40,000 fish—during January, February, and March at which time the fish were released.

It is considered probable that the continuing mortality was due to the same agent encountered at the Leavenworth station in 1951. Two other fish pathogens were isolated from moribund fish of this lot of fish at the Winthrop station during 1949–50 and tentatively identified as *Pseudomonas hydrophila* and *Ps. fluorescens*. Both produced fatal infections when injected into healthy fingerlings. While both may occur in nature as fish pathogens, it was believed that they were not a primary cause of the prevalent disease because, after the kidney infection was controlled, they did not occur consistently in infected fish (see Schäperclaus 1941, Layman 1949).

Material passed through a Seitz filter was used in tests for a filtrable agent in this group of fish. No evidence of a virus infection was demonstrated. A Seitz filter retains some viruses that will pass through Mandler filters. It will be recalled that in one experiment a Seitz filtrate of extracts of diseased fish from the Leavenworth outbreak was also noninfectious; in another, the agent passed through a Mandler filter and was shown to be infectious.

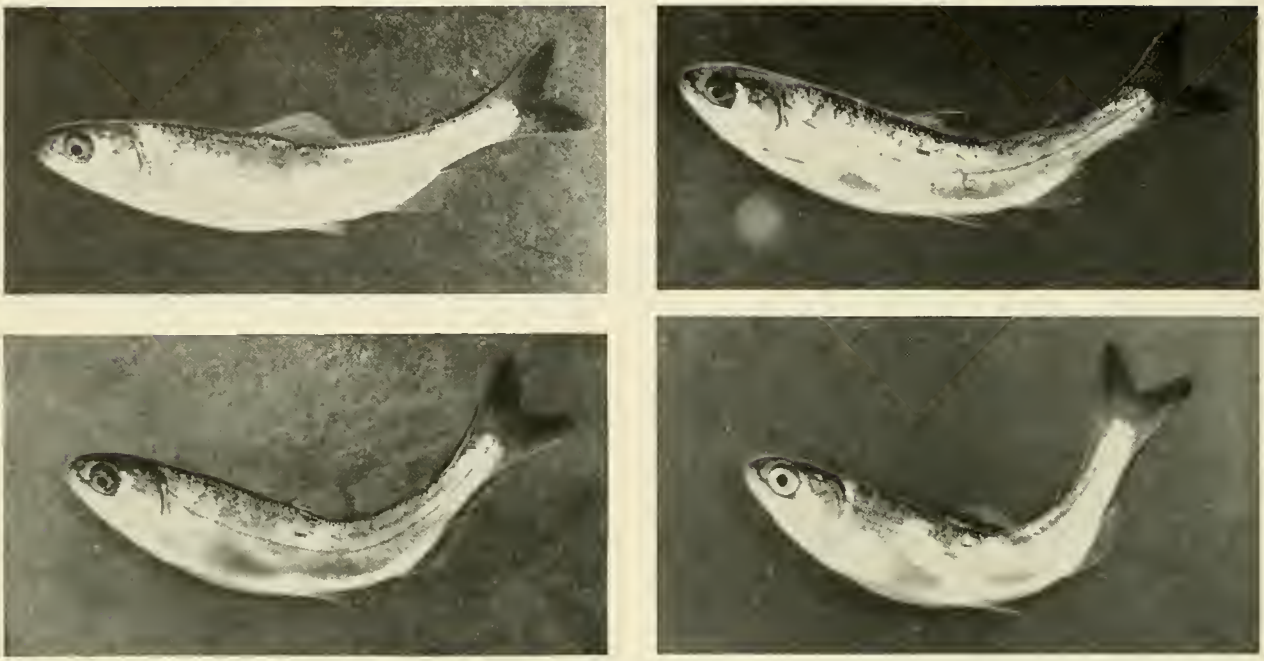

FIGURE 4.—Development of lordosis in a 3-inch kokanee injected intraperitoneally Sept. 30, 1951, with Mandler filtrate of suspension made from fish with lordosis and scoliosis. The first symptoms were observed on Nov. 3, and progression of the disease is shown in the photographs taken Nov. 9 (upper left), Nov. 16 (upper right), Nov. 23 (lower left), and Nov. 30 (lower right).

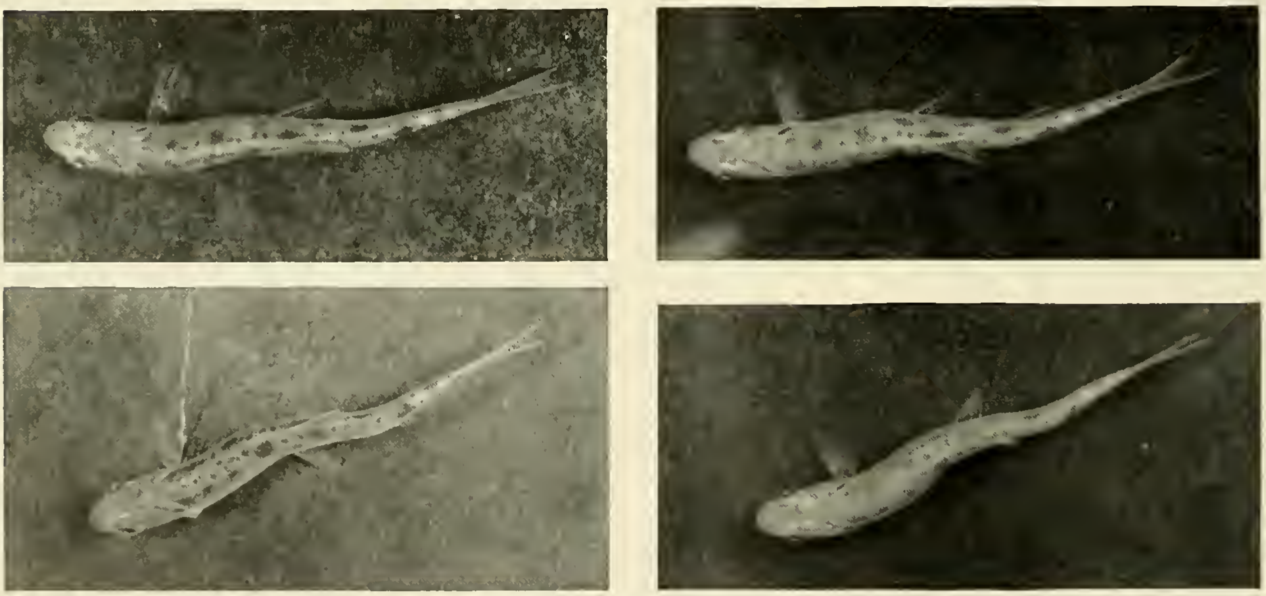

FIGURE 5.—Development of scoliosis in a 2-inch kokanee injected intraperitoneally Sept. 30, 1951, with Mandler filtrate of suspension made from fish with lordosis and scoliosis. The first symptoms were observed on Nov. 11, and progression of the disease is shown in the photographs taken Nov. 12 (upper left), Nov. 16 (upper right), Nov. 23 (lower left), and Nov. 30 (lower right).

BLUEBACK BROOD OF 1949

A group of about 140,000 small blueback-salmon fingerlings (Winthrop brood of 1949) showed a tremendous mortality at the Winthrop station during February 1950. These fish had hatched in January 1950, started feeding, and reached a length of about 1 inch in the month. The mortality occurred predominantly among the larger fish in the group.

The outbreak was characterized by a sudden increase in mortality. Most of the fish in an infected trough would die within a period of 2 weeks. The disease would appear in one trough, then show up in one or two others, gradually spreading from trough to trough, each suffering severe losses in its turn. Finally, the disease spread through the entire population. A loss of 80 percent in this group during the month of February was attributed to this disease.

Diseased fish were characterized by apathy, and they did not respond normally to moderate stimuli. A few fish developed scoliosis in March, and by May about 5 percent of the remaining stock of 2,000 fish showed this affliction. Scoliosis was not found among those that died during the earlier, acute stage of the epidemic.

At autopsy, small hemorrhagic areas visible through the peritoneum were common; they often extended into the muscle. Hemorrhagic areas at the base of the pectoral or pelvic fins and in the isthmus were frequent. Atrophy of the peduncle was noted in a few cases.

No significant organism could be found by direct examination nor could any be consistently isolated directly from these fish. A fluorescent pseudomonad was frequently recovered from the yearling bluebacks after they had become debilitated following injection of material from the small moribund fish. This was considered a secondary invader. The disease was infectious, as healthy yearling bluebacks were killed when injected with unfiltered and uncentrifuged saline extracts of the small moribund fish: and their appearance, while ill and at autopsy, resembled that of spontaneously infected fish. Seitz filtrates and heated material were innocuous.

KOKANEE BROOD OF 1949

The Winthrop station received 27,000, 2½-inch kokanee fingerlings, about 6 months old, from the Leavenworth station in October 1950. These fish had an insignificant loss at the Leavenworth station, but the mortality rate increased immediately upon arrival at Winthrop and the losses were high. The signs of the disease were similar to those of the bluebacks. All attempts to demonstrate an etiologic agent in tissue smears or by cultural methods failed. Nutritional deficiency was probably not of importance because similar fish at other stations on the same diet were not afflicted. Therapy by sulfonamides, antibiotics, and baths in disinfectants was of no benefit.

EXPERIMENTAL TRANSMISSION

Successful experimental transmission of the disease under natural conditions, using diseased fingerling bluebacks, was accomplished at the Winthrop station during the outbreak of March 1950. A screen partition was placed in a trough of diseased fish near the lower end of the trough, and about 4,000 diseased fish were held in the upper end. One hundred healthy chinook-salmon fingerlings (*O. tshawytscha*), 2 inches long and 4 months old, and 100 healthy blueback-salmon fingerlings, 1½ inches long and 3 months old, from disease-free stock at the Leavenworth station were placed in the lower compartment. During the next month 5 percent of the chinooks died from unknown causes. In the same period 95 percent of the bluebacks died showing evidence of the epizootic disease. They did not have the characteristic lesions of kidney disease and in our experience this bacterial infection has not been encountered in fish as small as those used in this experiment. Also, we have not transmitted kidney disease by contact or feeding experiments.

RELATION TO EPIZOOTIC AT LEAVENWORTH

The experiments and observations in transmitting the disease at Winthrop make it appear that a natural source of infection may be contaminated water. However, it is certain that during the 1950 epizootic at Winthrop, the water supply was not a continuing source of infection. Fish brought to the Winthrop station in March 1950 and cared for with equipment kept separate from the diseased fish did not contract the disease. Approximately 12,000 blueback fingerlings were shipped to Winthrop from Leavenworth on March 15, 1950, and an additional 50,000 on June 8. These fish averaged 1 and 1½ inches long, respectively, and had hatched during December 1949 and January 1950, from eggs of the Winthrop brood of 1949 shipped to the Leavenworth station in November 1949. They arrived at the Winthrop station during the epizootic, and were held with insignificant losses until the next spring when they were planted. It appears that neither the general water supply nor the food was a source of infection and that careful sanitary measures were effective in limiting the spread of the disease.

It is believed that the disease at Winthrop, although complicated by the presence of bacterial pathogens, was similar to the disease at Leavenworth. This is evidenced by the lack of response to sulfonamide, antibiotic, or pyridylmercuric acetate therapy, and by the similar pathology. Hemorrhagic areas were observed on the fins and body surface, and evidence of inflammation was seen on the air bladder, visceral fat, and intestine. The intestine was often congested and filled with a yellowish fluid, the stomach with a whitish fluid.

DISCUSSION

The literature on virus diseases among fish is not extensive and deals mainly with lymphocystis. The lymphocystis virus disease of fish is characterized by fibroblasts which have undergone an enormous hypertrophy. References can be found in an article by Alexandrowicz (1951) and articles by Weissenberg (1951), some dating back to 1914.

Layman (1949) decribed a virus disease called red disease of carp. The disease was produced experimentally in healthy carp by rubbing an abraded area with a bacteria-free filtrate prepared from the skin of diseased carp. The disease had an incubation period of 3 days in warm water and of 3 weeks in cold water. Usually the first victims were the ripe fish, but 2½- to 3-month-old and 10- to 11-month-old fish were frequently attacked. The diseased fish were characterized by apathy, erection of scales, ascites, popeye, skin ulcers, and protrusion of the anal region. The intestine was inflamed, and the feces were dense, partially transparent, and stringy. The liver and gall bladder were enlarged. The liver was light green and dark in parts and finally became partially necrotic. The spleen was somewhat enlarged and very anemic in appearance. An acute form of this disease developed in early spring and abated by summer, while a chronic form progressed throughout the summer until the end of September.

A disease described by Pacheco and Guimaraes (1933) was attributed to a filtrable virus. The disease was called cryo-ichtyozoose because the virus acted on fish at low temperatures. The virulence diminished or even disappeared entirely at a temperature higher than 16° C. (60.8° F.). The disease was characterized by a high mortality, apathy, congestion at the base of the pectoral fins, pale gills and viscera—especially the liver; a mucous secretion in the stomach and mouth; and bile that was sticky and amber-colored.

Magarinos Torres and Pacheco (1934) later described this disease as stomatitis and demonstrated cytoplasmic inclusions in epithelial cells from the floor of the mouth where cloudy swelling was present. They were dealing with the *Acara*, a fish in an entirely different order from that containing the salmon.

No inclusion bodies that could be regarded as indicating virus infection were encountered in the blueback-salmon or kokanee fingerlings studied in the present investigation. Occasional red spherical cytoplasmic bodies were seen in the epithelial cells of the mouth and a few other areas. These were usually from 2 to 5 microns in diameter. Such bodies were found a little more commonly in diseased fish than in healthy fish of the same age. They resemble closely the bodies that have been previously described in a variety of human conditions and were thought by some to be associated with specific virus infections. However, they have been shown to be commonly present in the pharyngeal epithelium of normal humans (Macaulay 1951).

It appears possible that the disease described by the South American investigators is the same as that described in the present paper. It should be noted that their work involved fish of a different order from those we studied. Whether the two diseases are the same cannot be determined from present evidence. Findings in the present study suggested that only fish of the species *O. nerka* were susceptible. Infection did not occur in *O.*

tshawytscha, O. kisutch, or *Salmo clarki clarki* exposed under conditions that caused a high infection rate in *O. nerka*. We are inclinded to believe that the South American disease is not the same as the one described in this paper.

Schäperclaus (1941) described a virus disease of rainbow trout, in which the fish became dark in color. The posterior third of the kidney was swollen, the surface corrugated. The head kidney was arched in shape and mealy, pulpy, or pasty in consistency. The musculature over the kidney was softened. The liver was often light, yellowish, or spotty in appearance. The gall bladder was normal in half the cases investigated, otherwise it was small and filled with a yellowish liquid. The anal region was sometimes swollen and protruding. The disease was produced among healthy fish by injecting filtered material from suspensions of both diseased kidneys and livers. The investigator reported that the course of the disease is slow and that 30 to 60 percent of rainbow trout can be lost during the normal rearing period. He cited one example in which 80,000 rainbow-trout fingerlings, 5 to 7 centimeters long, died in 14 days as a result of this disease.

The disease among the blueback-salmon and kokanee fingerlings at the Winthrop and Leavenworth stations seems to differ enough from any diseases previously described to warrant its consideration as a previously undescribed disease caused by a filtrable agent.

The development of scoliosis and lordosis among the blueblack-salmon and kokanee fingerlings is of interest. Schräder (1930) mentioned that spinal-column deformities are more common in fish than in all other vertebrates. He described the anatomical changes of a number of curvatures in fish and reviewed the literature. Factors attributed as causes of curvatures are heredity; an unequal development of muscle or its elasticity; parasitic infections in which muscle or cartilage is destroyed; nutritional deficiences as avitaminosis or lack of phosphorus or calcium; and oxygen deficiency, unfavorable temperatures or improper water balance in the developing egg.

McCay and Tunison (1934) found that brook-trout fingerlings raised on a diet containing one-third sheep plucks preserved in 1-percent formalin developed scoliosis after about a year when they were approximately 6 inches long.

SUMMARY

1. An investigation was made of a disease affecting blueback-salmon and kokanee fingerlings (*Oncorhynchus nerka*) at the Leavenworth and Winthrop stations in 1951. The disease did not infect fingerlings of the chinook salmon (*O. tshawytscha*), silver salmon (*O. kisutch*), or cutthroat trout (*Salmo clarki clarki*).

2. The disease was characterized at the beginning of an outbreak by a great increase in its infectious nature, and a resulting increase in the mortality of the fish.

3. The total mortality in a population of 800,000 to 1,400,000 salmon ranged from 11 to 40 percent. A decrease in the epizootic appeared to follow sterilization of cleaning equipment. The incidence of the disease decreased during summer months, and it was suspected that the higher water temperatures were a favorable factor.

4. The disease was produced by material that passed through bacteria-proof filters. The infection that was produced in healthy salmon by injection of suspensions made from moribund fish resembled the disease as it occurred naturally during the epizootic. Some injected fish developed scoliosis or lordosis. Results of the injection of salmon with heated material were negative.

5. The larger fish in a group were attacked first, becoming infected when they were 1 to 1.5 inches in length and about 3 months old.

6. Diseased fish were lethargic and often exhibited hemorrhagic areas at the base of the fins and in the isthmus. The stomach was distended with a milky fluid; and the intestine appeared reddened and contained a watery, straw-colored fluid often tinged with blood. The bile appeared normal, but in greater quantity than usual. Hyperemic areas frequently were present on the air bladder, peritoneum, or fat.

7. Spinal deformities developed in later stages among some of the fish that survived the early acute stage of the epizootic.

8. Experimental infection was accomplished by placing healthy fish in one end of a trough that contained sick fish in the upper compartment.

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SPAWNING OF YELLOWFIN TUNA IN HAWAIIAN WATERS

By FRED C. JUNE

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SPAWNING OF YELLOWFIN TUNA IN HAWAIIAN WATERS

By FRED C. JUNE, *Fishery Research Biologist*

The rapid growth of the Pacific tuna fisheries during the past several decades has focused attention on the biology of the various species that contribute to this industry. Studies are being made by the Pacific Oceanic Fishery Investigations, of the United States Fish and Wildlife Service, in those phases of the life history and habits of tunas which are basic to an interpretation of patterns of occurrence, movements, and dynamics of population numbers. Pertinent to such interpretation is the knowledge of the place, time, and extent of spawning.

Although records of spawning localities of tunas in the Pacific, based on collections of larvae and juveniles and the examination of gonads, have been furnished by various investigators (Marr 1948; Schaefer and Marr 1948; Wade 1950; Hatai, et al. 1941), knowledge of the extent of spawning in time for any particular locality and of the developmental changes that take place in the gonads concomitant with spawning is notably fragmentary.

The present paper deals with the spawning of the yellowfin tuna (*Neothunnus macropterus*) in Hawaiian waters, with particular reference to the reproductive process. Ova-diameter measurements have been used to demonstrate the developmental changes that take place in the gonads during the breeding season.[1]

Acknowledgment is made to Tamio Otsu, Richard Shomura, and Kenji Ego for their assistance in collecting data and making many of the ova measurements used in this paper, and to Tamotsu Nakata for preparing the various illustrations presented here. The author is also grateful to O. E. Sette and Dr. M. B. Schaefer for the time and advice they so freely gave him, and to Dr. A. L. Tester, University of Hawaii, for the many valuable suggestions offered him during the preparation of the paper.

COLLECTION AND TREATMENT OF OVARY SAMPLES

Because of the difficulty of determining and describing the relative maturity of the gonads from their external appearance, some objective measure of the growth of these organs that is associated with the breeding season was sought. The testes were not suitable because no quantitative measure of their sexual products could be found that would provide reasonably accurate estimates of their relative stages of development. While a relation was found between the size (weight) of the testes from individual fish and proximity of the spawning period in Hawaiian waters, variation in size of the testes among the fish examined was so great that no precise delineation of their growth changes could be obtained. Consequently, only the ovaries of female yellowfin tuna were used.

The material used in this study was obtained from yellowfin-tuna landings made in waters adjacent to the Hawaiian Islands by the commercial longline fishery. The ovaries were collected at the Kyodo Fishing Co., Ltd., of Honolulu, where the catches were weighed and sold at auction. Observations were made on 112 fish, or approximately 4 percent of the total number of yellowfin tuna landed at Honolulu between January and December 1950. The distribution, by dates, is given in table 1.

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[1] The use of ova-diameter measurements to indicate the growth that takes place in the ovaries prior to spawning was introduced by Thompson (1915) in his life-history study of the Pacific halibut. Clark (1925, 1929, and 1934) later applied the technique to spawning investigations of the jack smelt (*Atherinops californiensis*), the grunion (*Leuresthes tenuis*), and the California sardine (*Sardinops caerulea*). Other investigators also have used the method in spawning studies of several other marine species (Schaefer 1936; Olsen and Merriman 1946).

TABLE 1.—*Weight and stage of maturity of 112 yellowfin tuna from the Hawaiian longline fishery, January–December 1950*

Date	Body weight	Fresh ovary weight	Stage of maturity [1]	Date	Body weight	Fresh ovary weight	Stage of maturity [1]
	Pounds	*Grams*			*Pounds*	*Grams*	
Jan. 11	(2)	132.0	A	Aug. 11	124	1,051.7	F
11	98	154.0	B	15	117	996.4	F
11	99	154.0	A	21	152	1,354.7	E
11	97	149.0	A	29	108	1,292.0	H
26	110	154.7	A	Sept. 6	121	1,122.1	F
26	181	448.6	C	8	118	740.2	F
Feb. 1	94	143.4	A	18	194	2,823.3	F
2	117	188.6	B	25	171	1,121.3	F
8	144	317.7	A	Oct. 6	131	737.5	[3] F
10	96	139.1	A	6	191	1,146.3	[3] G
10	87	125.0	C	10	135	391.9	K
Mar. 17	119	293.1	B	10	164	1,938.0	F
21	116	240.0	A	12	171	(4)	E
24	92	191.4	B	13	125	561.0	[3] F
24	89	(4)	B	13	122	(4)	K
31	80	109.5	A	13	160	656.1	[3] E
Apr. 4	138	282.0	A	24	128	292.6	K
4	186	391.8	A	26	144	306.5	K
11	101	173.7	B	27	168	722.4	[3] F
11	151	365.7	A	31	130	235.3	A
15	(2)	156.4	A	31	124	254.2	A
27	143	429.7	C	Nov. 3	134	261.2	A
28	116	268.7	B	7	160	1,160.5	[3] G
28	131	320.0	A	9	138	321.7	K
May 5	(2)	(4)	F	10	122	182.1	A
9	119	314.3	D	16	162	479.4	A
June 6	154	729.8	[3] F	16	124	193.4	A
8	113	1,176.0	G	24	150	250.3	A
8	130	1,047.5	G	24	147	231.6	A
13	126	1,121.5	F	26	149	247.2	A
14	121	1,712.0	J	29	174	290.0	A
14	109	357.6	D	29	146	229.5	A
20	172	2,565.2	F	30	107	185.6	A
20	135	(4)	F	30	119	228.6	A
22	125	1,317.3	F	30	130	231.2	A
23	131	872.6	F	30	142	272.7	A
26	124	1,010.9	G	Dec. 1	112	185.1	A
26	126	988.5	F	1	136	214.3	A
28	137	1,326.8	H	4	138	230.4	A
29	136	1,084.9	F	6	125	236.3	A
29	157	1,404.4	I	6	145	253.8	A
July 3	104	751.6	F	6	143	204.2	A
5	116	981.7	E	6	146	225.5	A
7	130	1,571.6	F	11	150	260.9	A
11	107	1,127.6	H	12	118	153.6	A
12	143	1,620.7	F	13	156	337.0	A
12	105	1,112.3	F	13	130	252.7	A
14	124	1,364.4	F	16	134	271.0	A
19	132	1,386.1	F	16	97	134.8	B
25	121	848.3	E	15	150	283.1	A
26	134	906.2	F	15	143	324.4	O
28	153	1,536.8	G	19	208	485.7	A
Aug. 1	119	545.7	[3] F	20	136	250.6	A
3	147	1,236.0	F	26	159	286.4	A
3	177	1,628.4	F	27	145	305.9	A
10	173	2,791.9	I	28	110	160.8	A

[1] For classification of the stages of maturity, see p. 51.
[2] Fish weights unavailable.
[3] Maturing ovaries in which some ova had been lost through previous spawning earlier in the season.
[4] Ovaries not intact.

Longline gear appears to select the larger, adult fish; hence, the smaller, sexually immature fish are not represented in the collections, which include the size range 36.3 to 94.3 kilograms (80 to 208 pounds).[2]

The date, weight of fish, locality of capture, and state of sexual maturity, based on the criteria established by Marr (1948), were recorded for each sample. The ovaries, together with attached peritoneal and vascular tissues, were carefully removed from the fish. The posterior end of each ovary was severed at its juncture with the oviduct, and after all superfluous tissues were removed, the ovaries were weighed on a triple-beam balance to the nearest 0.1 gram and placed in 10-percent formalin.

Preliminary test measurements were made on samples of 300 ova from the anterior, central, and posterior parts of both ovaries from a near-spawning fish to determine whether the ova matured at the same rate and in the same relative numbers throughout the ovaries. An analysis of variance and a chi-square test (Snedecor 1946) showed no significant differences either in the mean diameters of ova ($P>0.05$) or in the relative numbers of ova in each size group ($P=0.70$) from these three regions of an ovary. Furthermore, no significant differences were found in ova size between the two ovaries from the same fish. Similar measurements were made for an immature ovary, and no significant differences were found, either among the different parts of the same ovary or between ovaries from the same fish. Thus, it was concluded that the ova develop uniformly throughout the ovary and in both ovaries of a fish. All further ova samples for this study were taken from the middle of the left ovary and are considered representative of both ovaries.

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[2] Yellowfin tuna weighing between 15 and 60 lbs. are caught rather infrequently in Hawaiian waters. Longline gear, which is specifically designed to capture large fish, seldom takes yellowfin tuna smaller than 60 lbs. Trolling gear, which is less selective of fish size, catches very few of the 15-to-60-lb. size group, even though the amount of fishing effort is substantial throughout the year. Small yellowfin tuna from 2 to 20 lbs., but no larger, sometimes are captured in great numbers by the pole-and-line bait fishery for skipjack. The virtual absence of the maturing size group (15 to 60 lbs.) in the Hawaiian tuna landings suggests that most members of this segment of the population migrate elsewhere to mature, and only the adult sexually mature fish frequent local waters.

The samples were taken after the ovaries had hardened in formalin. Ova from a sample were teased out under a binocular microscope to ensure complete separation from the follicles. After the ova were stirred in a watch glass, a small subsample was drawn with a pipette and placed on a glass slide for measurement. Parallel markings with 1-millimeter spacing on the slide were an aid in avoiding duplicate measurements of the same ovum. Measurements were made by an ocular micrometer in a compound microscope at a magnification of six diameters. Although the ova seldom were perfectly spherical, measurements were made on whatever axis fell parallel to the micrometer graduations. This method of measurement has been used by other investigators (Clark 1925, 1934; Schaefer 1936) and, on the basis of comparative test measurements of ova made before and after their preservation, it was found reliable in the present study.

Maturing ovaries contain not only the translucent, immature ova, but also several groups of larger sizes. To ensure adequate numbers of these latter groups without extravagant expenditure of time on the much more numerous immature ova, measurements were made on 300 ova larger than 0.16 mm. in diameter for all maturing ovaries. For ovaries in the immature stage, 200 ova were measured.

DESCRIPTION OF THE OVARIES

The ovaries of sexually mature yellowfin tuna are paired, elongated organs that extend nearly the length of the abdominal cavity. They are approximately round in cross section and almost symmetrical—the left ovary usually being slightly larger than the right. The ovaries are suspended from the dorsal wall of the body cavity by a fold in the peritoneum. Posteriorly, the ovaries unite, with the lumina joined to a short, wide oviduct that opens as a slit on a papilla behind the anus. Anteriorly, the ovaries receive their blood supply from two of the three branches of the coeliac-mesenteric artery; the No. I branch apparently nourishes the left ovary and the No. III branch the right ovary (Godsil and Byers 1944). As the time of spawning approaches, the superficial blood vessels supplying these organs become enlarged and very conspicuous.

DEVELOPMENT OF THE OVA

Within the ovaries of sexually mature fish, several developmental groups of ova may be distinguished at one time or another through the year. On the basis of the characteristics of the largest ova present, the ovaries were classified into the following stages of maturity:

Immature: Immature ovaries contain ova ranging from 0.01 to 0.18 mm. in diameter, with a mode of about 0.08 mm. Preserved in formalin, the ova are translucent, spherical bodies, and are invisible to the naked eye. Each ovum contains a rather large, vesicular, eccentric nucleus enclosed in a clearly defined nuclear membrane. Ova of this group are present in the ovaries throughout the year. Fresh ovaries at this stage are pinkish, elongated, and slender.

Intermediate: Ovaries at this stage contain ova which range from about 0.18 to 0.40 mm. in diameter. As the ovum increases from about 0.18 to 0.40 mm., the nucleus enlarges and the yolk granules appear. The cytoplasm containing the scattered, spherical yolk granules is enclosed by two membranes. The innermost of these, the vitelline, or fertilization, membrane, can be clearly distinguished only in the mature ovum. A comparatively tough, thin, and shell-like outer membrane, the zona radiata, is in direct contact with the surrounding ovarian follicle during development of the ovum. The zona radiata is transparent and sculptured with very fine striations on its outer surface. This membrane is clearly evident at all stages of maturation. Formalin-preserved ova in this group are semiopaque and are barely distinguishable without magnification. Fresh ovaries containing ova which have developed to the intermediate size are indistinguishable in appearance from those containing only immature ova.

Maturing: As the ova advance toward maturity, the group, beyond about 0.40 mm., becomes opaque and exhibits a characteristic yellowish color in formalin. The yolk granules appear as highly refractive, spherical bodies in the cytoplasm. At this stage of development, the fresh ovaries are conspicuously turgid, yellowish in color, and the ova are firmly embedded in the follicles.

To demonstrate the size distribution of the intermediate and maturing ova groups, a sample of tissue (0.5 gm.) was taken from a maturing ovary of a fish landed in early May. After separation of the ova from the follicles, measurements were made of all ova above 0.18 mm. in diameter in the sample. Their diameter frequency distribution, shown in figure 1, clearly indicates the presence of several groups which simultaneously are developing to maturity. Two chief groups are distinguishable: Intermediate, from 0.18 to about 0.40 mm.; and maturing, beyond 0.40 mm., which itself appears to consist of more than one group.

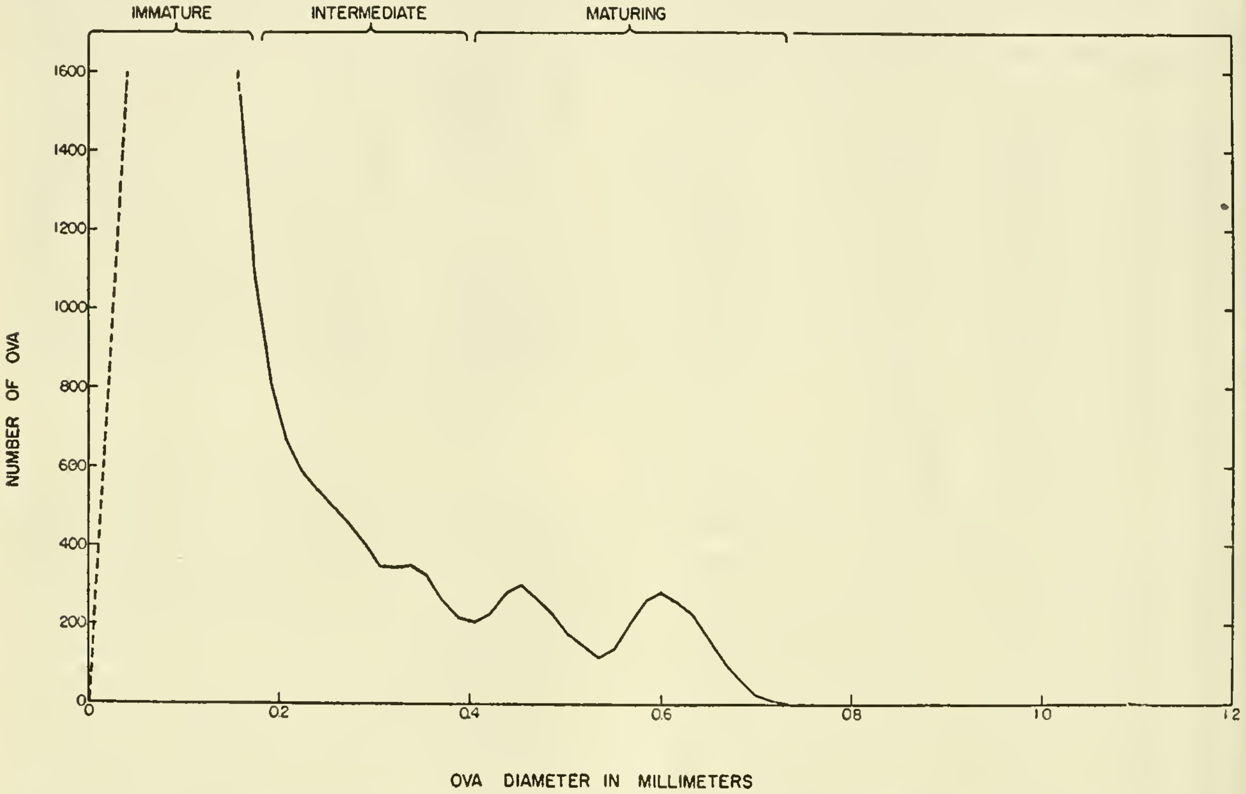

FIGURE 1.—Frequency polygon of 12,041 ova diameters measured from a maturing ovary of a yellowfin tuna taken in Hawaiian waters, May 5, 1950. Only ova measuring more than 0.18 mm. in diameter were included.

Ripe: On reaching the stage at which the ova are about to be spawned, distinct morphological changes occur in them, and they lose their opacity and assume a translucent, grayish color in formalin. Ripe ova measure about 0.76 to 1.23 mm. in diameter. Embedded in the yolk is a single, conspicuous, golden-yellow oil globule, which averages about 0.26 mm. in diameter. Ripe ova readily break from the follicles in which they develop, collect in the lumina of the ovaries, and flow freely from the oviduct when the sides of the fish are pressed.

To show further the size distribution of these developmental groups, a frequency distribution

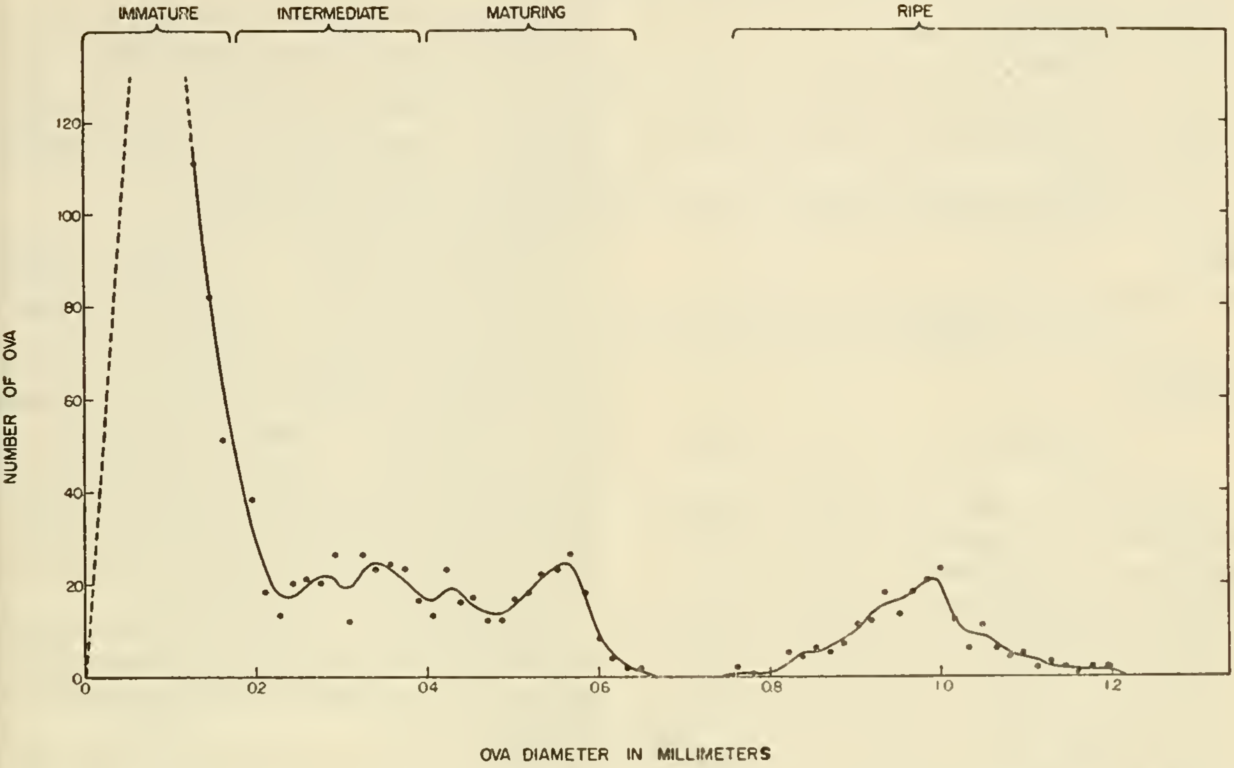

FIGURE 2.—Frequency curve of 1,000 ova diameters measured from a ripe ovary of a 121-lb. yellowfin tuna taken in Hawaiian waters, June 11, 1950. Only ova measuring more than 0.13 mm. in diameter were included. The line represents the original data (dots) smoothed by the formula $\frac{a+2b+c}{4}$

was made of 1,000 ova more than 0.13 mm. in diameter taken from a ripe ovary (fig. 2). The group with diameters measuring from 0.76 to 1.23 mm. includes ova almost ready for spawning, and it can be easily distinguished from the intermediate and maturing groups below 0.65 mm. in diameter. The immature group is indicated in figure 2 by a dotted line.

Spawned out: Toward the end of the spawning season the ovaries decrease in size, become hollow and flaccid, and gradually resume the appearance of those in the immature stage. Following spawning, ripe ova remnants in various stages of degeneration are found in the lumina of the ovaries. Ova in the intermediate and maturing groups which remain in the follicles at the conclusion of spawning take on a deep greenish or brownish color in formalin, and the yolk granules appear as dark specks, indicating that these ova are degenerating and undergoing absorption. During the spawning season ripe ova remnants often are present in the lumen of the ovary at the same time that the ovary is still very much enlarged and apparently maturing a group or successive groups of ova.

Since the previously noted developmental groups marking maturation of the ova were clearly evident, and since these groups showed intergradation in fish collected at different times through the year, the ova-diameter frequency polygons of each sample in the collection were classified according to the position of the mode of the most mature group of ova present. The following 11 arbitrary stages were defined:

Immature

Stage A: Mode at about 0.08 mm., no ova above 0.18 mm.

Intermediate

Stage B: Mode of the most mature group below 0.29 mm.; no ova above 0.34 mm.

Stage C: Mode of the most mature group between 0.29 and 0.39 mm.

Maturing

Stage D: Mode of the most mature group between 0.39 and 0.49 mm.

Stage E: Mode of the most mature group between 0.49 and 0.59 mm.

Maturing (Continued)

Stage F: Mode of the most mature group between 0.59 and 0.69 mm.

Stage G: Mode of the most mature group between 0.69 and 0.79 mm.

Stage H: Mode of the most mature group between 0.79 and 0.89 mm.

Stage I: Mode of the most mature group between 0.89 and 0.99 mm.

Ripe

Stage J: Mode of the most mature group at about 1.00 mm.; some ova segregated in the lumina of the ovaries.

Spawned out

Stage K: Ovaries with a few loose ova in the lumina, including some which are undergoing degeneration.

These stages are shown graphically in figure 3 which has no connotation of time, but simply illustrates the developmental stages from the immature, or resting, stage to the spawning stage. With the exception of stage J, which is represented by the ova from only one fish, the polygons are pooled frequencies of several fish of the same maturity classification. The number of individuals included in each frequency is indicated at the right. Except for stage A, the pooled frequencies were reduced to the basis of 300 ova (the number measured from each fish).

Ripe ovaries from only one female yellowfin tuna were present in the 1950 collections. Furthermore, examples of the preceding two stages of maturity, H and I, totaled only six among the fish sampled, suggesting perhaps that, during or just before spawning, yellowfin tuna bite less on the longline hooks or migrate to an area or a depth not being fished. Schaefer and Marr (1948) offered these hypotheses to account for the absence of spawning yellowfin tuna in the live-bait boat catches in the waters off Costa Rica during their investigations in 1947.

It may be seen in figure 3 that as the last group of ova evident in the frequency polygons progresses toward maturity, a second group becomes differentiated and also progresses toward maturity. The progression of the modes of these successive groups is more evident in figure 4, where the frequency distributions from figure 3 are expressed as deviations from the average frequency polygon of stages B through J. The deviations were smoothed twice by a moving average of 3 to remove chance fluctuations. In this form, the maturing group at about 0.30 mm. in stage C and at 0.45 mm. in stage D can be clearly distinguished by appearance from the immature group. Furthermore, the deficit of 0.20-mm. ova, beginning with stage E, suggests that fewer ova develop from the immature group into the intermediate group after stage D than before.

The progression of the two right-hand modes is compared in figure 5 by a scatter diagram wherein the position of the mode of the last group (Y) is plotted against the position of the mode of the preceding group (X) for each of 44 fish with ovaries in stages E through J. The locations of the modes were determined by inspection of the deviations of the individual frequencies from the average frequency polygon. A coefficient of correlation of 0.855 (P is considerably less than 0.01) emphasizes the close relation between the progression of succeeding modes.

The multiplicity of modal groups and the high correlation between modes of successive ova groups strongly indicate that individual fish spawn more than once a year.

Further support of the hypothesis that more than one group of ova is matured by individual fish during the spawning period arises from the presence of semitransparent, mature ova lying loosely in the lumina of the ovaries at the same time that a second group of ova is developing toward maturity. Among these remnants, some of the ova were grayish in color with the shell membranes partially collapsed; in a few, the oil globules were still discernible; and in others, only the transparent shell membranes or fragments of the shells remained. That these remnants are not carried over from the previous year's spawning is evidenced by the fact that ovaries in the resting, or immature, stage (stage A) and those in the intermediate stages of maturity (stages B and C) which were collected at the beginning of the year showed no signs of ova remnants in the lumina from recent spawnings. Furthermore, the condition of the mature ova remaining in the ovaries, as previously described, indicates that the group of which they were a part probably had been extruded only a short time before. Finally, among fish with ovaries in the maturing stages, eight samples in stages E, F, and G were found in which the ovaries were very much enlarged and turgid and in which remnants of mature ova were scat-

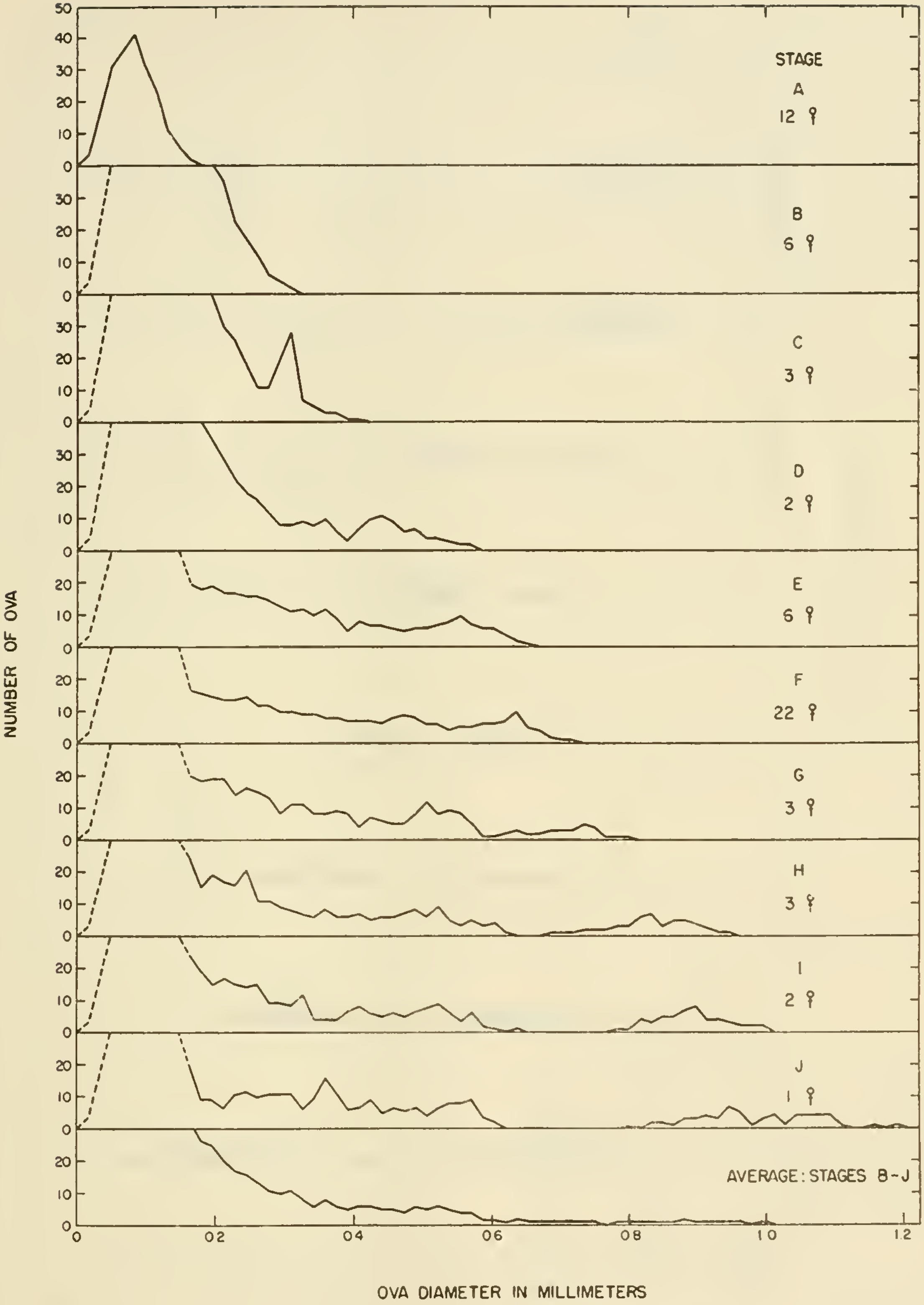

FIGURE 3.—Ova-diameter frequency polygons showing stages in development of the ova from the immature, or resting, stage to maturity.

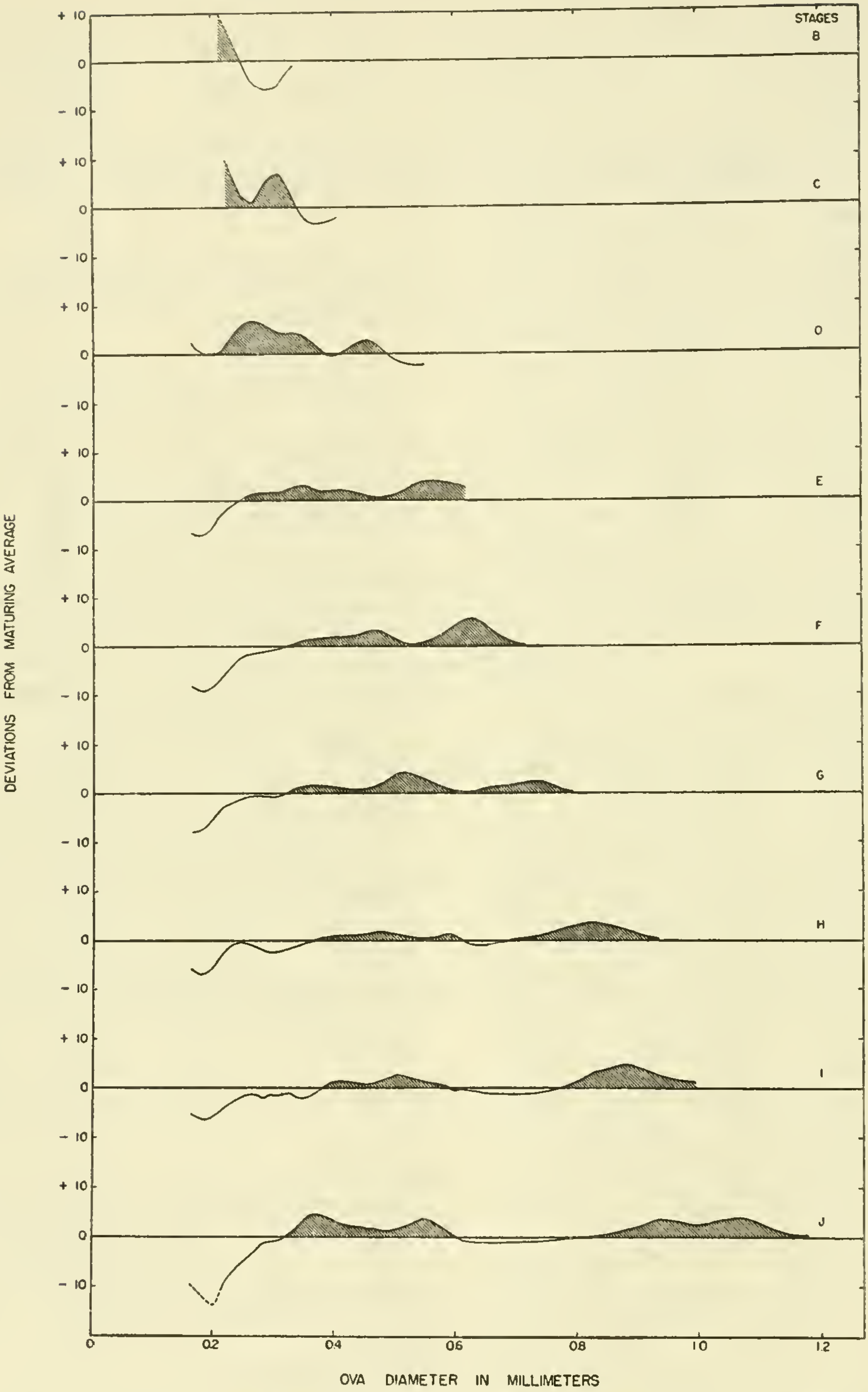

FIGURE 4.—Deviations from the average frequency polygon of stages B through J. The deviations were smoothed to minimize chance fluctuations.

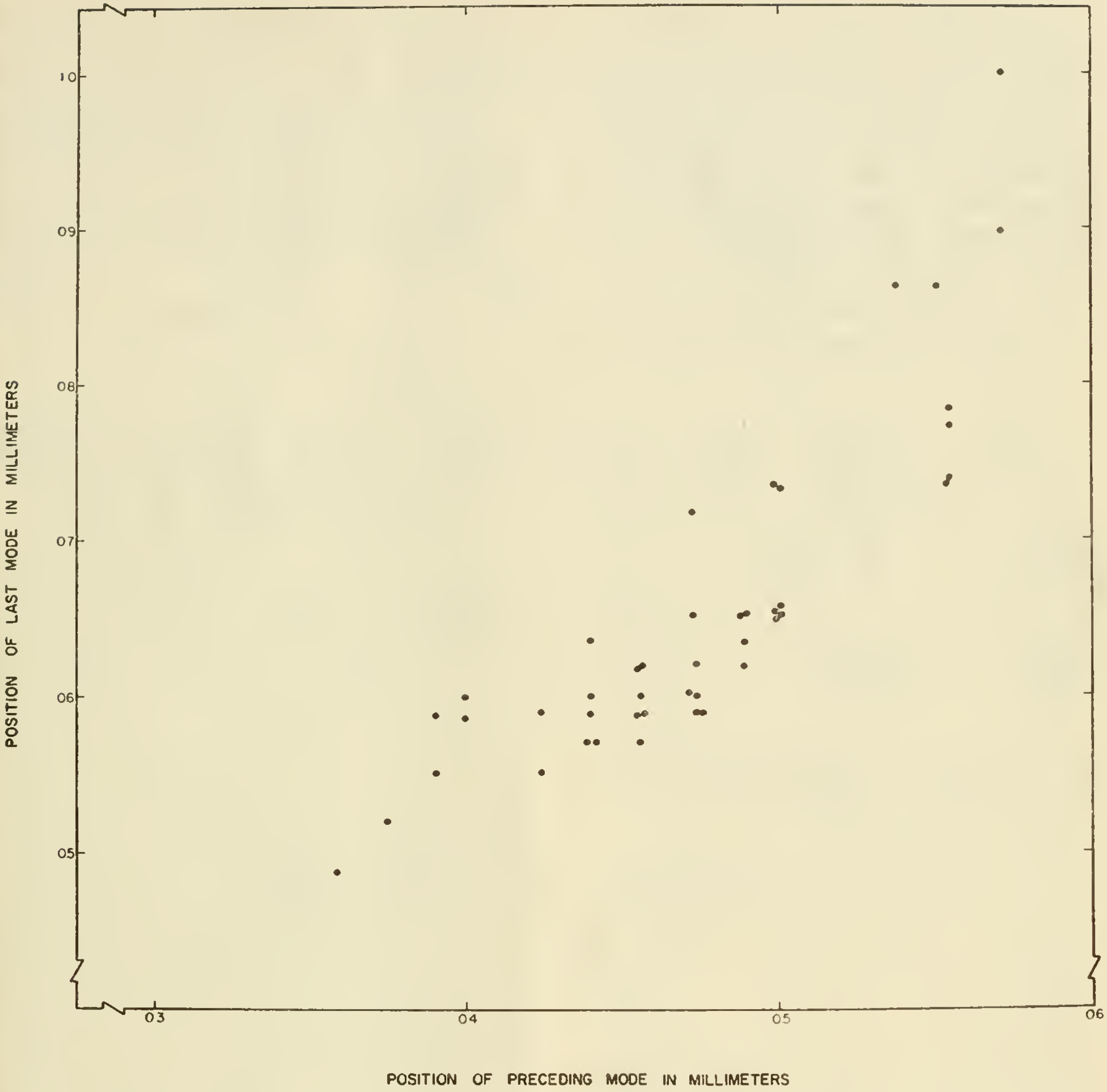

FIGURE 5.—Scatter diagram showing relation between modal groups of ova in the ovaries, stages E through J.

tered in the lumina. Of these eight samples, one was collected in June, one in August, five in October, and one in November. Thus, the presence of ova remnants in ovaries which show every indication of future spawning gives further evidence in favor of the hypothesis that more than one group of ova is matured and spawned by an individual fish in a single breeding season.

It is suggested in figure 3, by the trough at about 0.2 mm. in stages E to J, that many ova graduate from the immature to the intermediate group in stages A to D and few in stages E to J. In table 2 we find that fish with ovaries in stages A to D occur from November to May, tapering down to very few by June. This distribution of stages A through D suggests that the intermediate group should be found in largest number by early summer. Thereafter, if the intermediate group furnishes successive groups of ripe ova, the number of ova in the immature group should decrease. To determine whether the latter was true, comparisons were made of the ova-diameter frequency polygons for 23 fish in stage F according to the months in which they were collected. The number of ova larger than 0.55 mm. in diameter was compared with the number of those measuring between 0.18 and 0.53 mm. Ratios of the numbers of ova comprising intermediate and maturing groups for all fish in stage F are shown in table 3. It may be seen that in June the ratios ranged between 4.36 : 1 and 5.98 : 1, the average being 5.08 : 1. For July the average ratio, 4.50 : 1, was slightly less. It declined more in August (3.80 : 1) and still more in September (3.25 : 1).

To determine the consistency in each month of the ratios obtained for fish with ovaries in stage F, the chi-square test was used. No significant interaction (the smallest probability value obtained was about 0.70) was found among the individual samples collected during any one month; therefore, the pooled data for each month were used to test the consistency of the ratios among the 4 months, June through September. As shown by an interaction chi square of 27.72 ($P<0.01$), according to the method of Snedecor (1946, sec. 9.10), from the data presented in table 4, it is unlikely that the monthly ratios were drawn from a homogeneous population. Thus, there is a significant decline in the ratios of the maturing to the intermediate group through successive months.

This is not due to a change in the size of fish during the season. It is seen in table 3 that the mean weights of yellowfin tuna with ovaries in stage F did not change appreciably during the period considered. By an analysis of variance, it was found that among these samples, the difference between months was not more significant than the difference within months ($F=1.31$; $P>0.05$). In other words, the population did not change significantly as to size during the season. Thus, if the change is not connected with size of fish, it doubtless reflects a decline in proportionate numbers of ova composing the intermediate groups.

TABLE 2.—*Distribution by months of fish with ovaries in the various stages of maturity*

Month	Stages of maturity																						Total number
	A		B		C		D		E		F		O		H		I		J		K		
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	
January	4	66.7	1	16.7	1	16.7																	6
February	3	60.0	1	20.0	1	20.0																	5
March	2	40.0	3	60.0																			5
April	5	62.5	2	25.0	1	12.5																	8
May							1	50.0			1	50.0											2
June							1	6.7			8	53.3	3	20.0	1	6.7	1	6.7	1	6.7			15
July									2	18.2	7	63.6	1	9.1	1	9.1							11
August									1	12.5	5	62.5			1	12.5	1	12.5					8
September											4	100.0											4
October	2	15.4							2	15.4	4	30.8	1	7.7							4	30.8	13
November	13	86.7											1	6.7							1	6.7	15
December	18	90.0	1	5.0	1	5.0																	20
Total	47		8		4		2		5		29		6		3		2		1		5		112

TABLE 3.—*Ratios of ova between 0.18 and 0.53 mm. to ova larger than 0.55 mm. for all fish with ovaries in stage F, June–September 1950*

Date	Fish weight	Ratio
	Pounds	
June 6	154	5.00:1
13	126	4.36:1
20	135	4.45:1
22	125	4.66:1
23	131	5.12:1
26	126	5.98:1
29	136	5.98:1
Average ratio		5.08:1
July 3	104	5.12:1
7	130	3.84:1
12	143	3.76:1
12	105	4.66:1
14	124	4.36:1
19	132	4.77:1
25	134	5.00:1
Average ratio		4.50:1
Aug. 1	119	3.84:1
3	177	3.48:1
3	147	3.84:1
11	124	4.17:1
16	117	3.69:1
Average ratio		3.80:1
Sept. 6	121	3.11:1
8	118	3.54:1
18	194	3.35:1
25	171	3.00:1
Average ratio		3.25:1

This decline is to be expected if there are successive spawnings by each fish.

TABLE 4.—*Proportionate numbers of ova more than 0.38 mm. in diameter for all fish with ovaries in stage F, June–September 1950*

Month	Total number of ova	Number of ova over 0.38 mm. in diameter	Probability of ova over 0.38 mm. in diameter [1]
June	2,100	349	0.166
July	2,100	385	0.183
August	1,500	313	0.209
September	1,200	283	0.236

[1] The ratio of pooled ova in the two groups for each month.

In summary, the presence of several groups of ova in the maturing ovaries as indicated by the ova-diameter frequency polygons, the significant correlation between successive groups of maturing ova, the presence of remnants of mature ova from a previous spawning in the lumina of the ovaries at the same time that successive groups are maturing, and the decrease in the proportionate numbers of ova composing the intermediate group as the spawning period progressed appear to be ample evidence that individual yellowfin tuna spawn more than once during the breeding season in Hawaiian waters. However, from this study, it is not possible to give any estimate of the number of times an individual fish may spawn during the season or the period of time that elapses between spawnings.

Among ovary samples collected during November and early December 1950, after spawning had terminated, were several with scattered remnants of mature ova in the lumina, indicating that the fish had spawned the previous summer or fall. Except for these remnants, which consisted of shells, some with the oil globules still discernible, only immature ova were present. Ovaries collected during January, February, and March, 1950, contained only immature ova, and no remnants were evident. Thus, it appears that ova in the intermediate stage at the close of the spawning period are absorbed and are not carried over to the following year.

RELATION OF OVARY SIZE TO FISH SIZE AS A MEASURE OF MATURITY

Having defined the stages of maturity according to the position of the mode of the most mature group of ova in the ova-diameter frequency distributions, the question then arises: Is there some simpler technique by which these stages might be approximated without the laborious measurements of ova diameters? If a relation exists between ovary weight at particular stages of maturity and fish weight (as a measure of fish size), it would be possible to compare the changes in the growth of the ovaries for fish of comparable sizes.

One means of estimating this relation is to determine the percentage that the ovary composes of the total weight of the fish. This method was used by Hoek (1895) as a measure of the degree of ripeness in Rhine salmon. Masterman (1913a and 1913b) later applied the method for estimating sexual maturity in European salmon and smelt (*Osmerus eperlanus*). Others investigating the spawning of the European salmon have followed Masterman. This method also has been used to a certain extent by Olsen and Merriman (1946) in their study of the spawning of the ocean pout (*Macrozoarces americanus*) in the North Atlantic.

While the relation of the ovary weight to the body weight gave a fair approximation of relative maturity in the yellowfin tuna, the ratio expressing this relation was not directly proportional over the size range of fish for a particular stage of maturity. When ovary weight was plotted against body weight,[3] great variation among the ovary weights was found for fish of a particular size. These observations appeared to fall into two generally distinct groups, one consisting of fish with ovaries in the immature stages (A, B, and C) and the other consisting of fish with ovaries in the maturing and ripe stages (D through J); although some of the values were intermediate between the two groups.

The relation between body weight and ovary weight for the immature and intermediate stages of maturity (A, B, and C) was found to be linear over the ranges of fish size and ovary size. Furthermore, when weights of ovaries in stages B and C were plotted against fish weights, the resulting regression was nearly identical with the linear regression obtained for fish with ovaries in stage A. Covariance analysis indicated that the two regression coefficients were sufficiently similar ($F=2.30$; $P>0.05$) to warrant the assumption that they arose from a single homogeneous group

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[3] Both fish and ovaries were weighed while fresh.

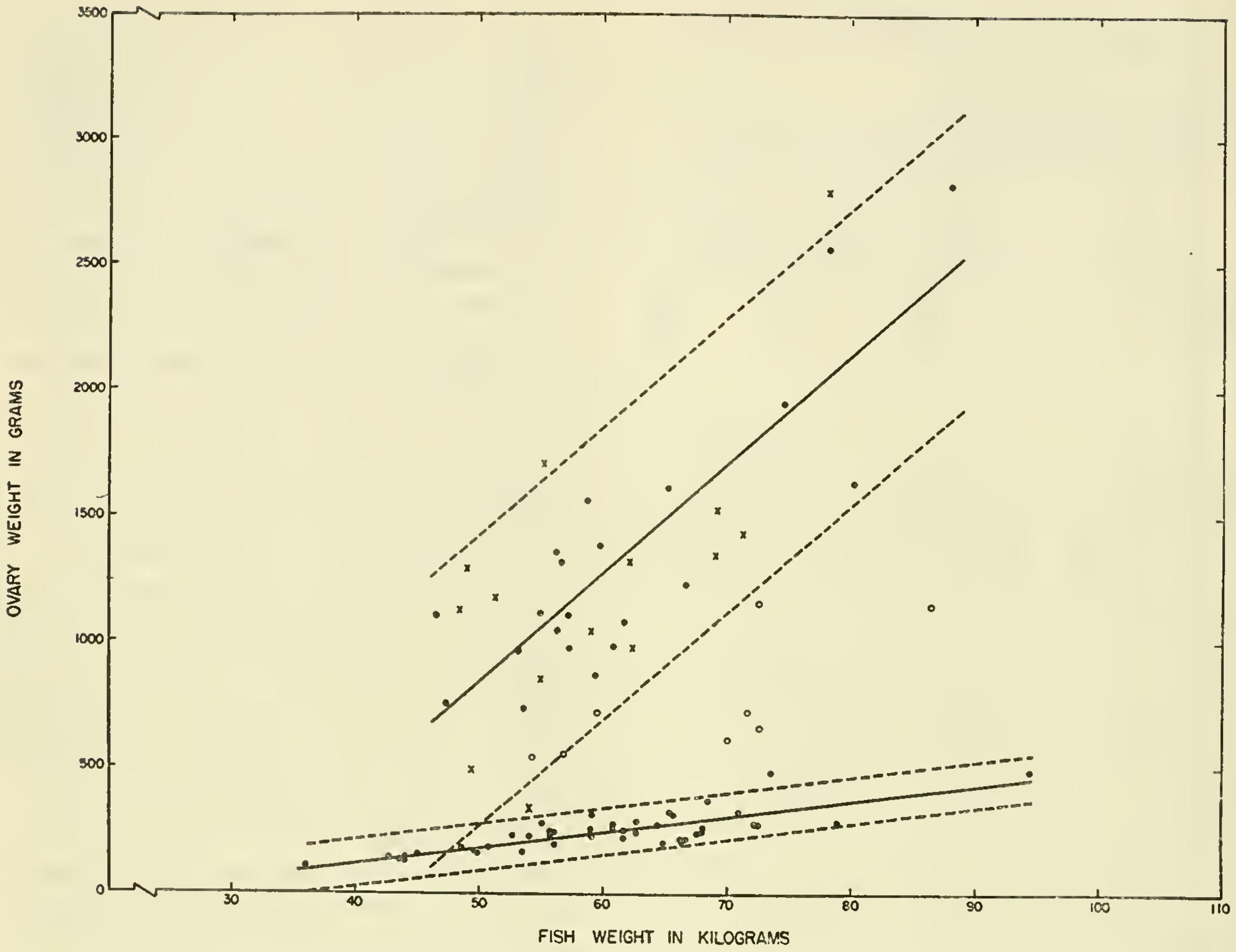

FIGURE 6.—Ovary weight-fish relation for yellowfin tuna with ovaries in stages A and F. The lower curve represents fish with ovaries in the immature, or resting, stage (A), and the upper curve represents fish with ovaries in a maturing stage (F). An x indicates an individual with ovaries in a maturing stage other than F; a circle indicates a fish which has spawned during the season.

(table 5). There was a significant difference in the level of the line representing stages B and C from that representing stage A ($F=13.73$; $P<0.01$), but the mean difference of the observed ovary weights was only 61.7 grams. Because of the significant difference in the levels of the two lines and because there were only eight ovaries in stage B and four in stage C, these were excluded from the linear regression of ovary weight on fish weight for the immature stage. The plotted data for stage A, shown in figure 6, were found to be best fitted by the equation

$$Y=6.0929X-124.35$$

where Y is ovary weight in grams and X is fish weight in kilograms. The dashed lines drawn parallel to the regression line represent plus and minus twice the standard deviation from regression.

TABLE 5.—*Tests of significance among adjusted means and between the regression coefficients of ovaries in stage A and in stages B and C*

Source of variation	Degrees of freedom	Sum of squares	Mean square
Total deviations from pooled linear regression	55	123.99888	----------
Deviations from average regression within samples	54	98.85509	1.83065
Deviations from individual regressions	53	94.74937	1.78772
Difference between regressions	1	4.10572	4.10572
Difference between adjusted means	1	25.14379	[1] 25.14379

[1] Highly significant.

As noted previously, there is an obvious increase in ovary weight as the ova develop to the maturing stages. The group of data shown in the upper part of figure 6 represents fish with ovaries in the ripe and maturing stages of development, D through J. Because stage F (shown by dots) was the only maturing stage which was well represented in the collection, it was used to describe the relation between ovary weight and fish weight at the approach of spawning. Over the ranges of fish size and ovary size, the regression of ovary weight on fish weight for ovaries in stage F[4] was found to be best described by the linear equation

$$Y=43.4811X-1327.8573.$$

The regression coefficient had a standard error of 6.060. The lines drawn parallel to the regression line indicate plus and minus twice the standard deviation from regression.

It is evident from figure 6 that the slopes and levels of the two regression lines, one representing fish with ovaries in the immature, or resting, stage (A) and the other representing fish in a maturing stage (F), are significantly different. The difference in slope is due to the fact that in stage F the larger fish tend to have relatively larger ovaries. The difference in level reflects the increase in size of the ovaries between stage A and stage F.

The values representing fish with ovaries in other maturing stages (D, E, G, H, and I) and the ripe stage (J), and those in which there was no evidence of previous spawning, are indicated in figure 6 by an x. Unfortunately, there are too few samples in any one of these stages to establish a regression with any degree of confidence. From the fact that most of the values for these stages lie within two standard deviations of the regression line for stage F, it appears that when the ovaries reach stage D they have already greatly increased in weight over stage A and that they increase very little while progressing through stages D, E, F, G, H, and I. The paucity of samples of all of these stages except F also suggests that the stages, other than F, probably are passed through very rapidly. The scarcity of some of the younger stages such as D and E might be ascribed to undersampling in May, but irregularity of sampling can scarcely explain the consistent dominance of stage F over all other stages during June to September. This dominance seems most reasonably explained by stage F being relatively long and stable and the other stages being transitory and rapidly passed. For practical purposes, then, but two groups need be recognized: (1) Fish with ovaries in stages A, B, and C, or in nonspawning condition; and (2) fish with ovaries in stages D to J, or in spawning condition.

For those ovaries in maturing stages in which some spawning had occurred during the season (remnants of mature ova were in the lumina), the points fall somewhere below the upper line but lie above the lower line. These are shown as circles in figure 6.

With respect to time of year, the regression for ovaries in stage A expresses the relation between ovary weight and fish weight during the off-breeding season (November through April), and the regression for ovaries in stage F expresses the relation during the spawning period (mid-May through October) as indicated by these data. (See Spawning Season, p. 61.)

Thus, by utilizing the scatter diagram of figure 6, it is possible, over the size range 36 to 94 kg. (80 to 208 lbs.), to determine whether an individual yellowfin tuna is in nonspawning or spawning condition by simply locating on figure 6 the coordinates of the weight of its ovaries and of its total weight. The coordinates will probably cross within one set of dashed lines or the other and the fish may be appropriately identified as nonspawning or spawning; some fish will fall at intermediate coordinate points—they are most probably in spawning condition and have already extruded some ova.

It is of interest that some discrepancy was found between the classification of the ovaries on the basis of their external appearance and their classification on the basis of the arbitrary stages of maturity established by ova-diameter measurements. It will be recalled (p. 48) that at the time of collection, the relative maturity of each ovary sample was recorded according to the stages established by Marr (1948). Among the 112 samples in the collection, this subjective method of classification resulted in 13 fish with maturing ovaries being incorrectly identified as spawned out, or roughly, in an error of about 10 percent. The greatest source of error was among those ovaries in stages E and F in which some spawning had taken place during the season. On the whole, however, if Marr's definitions were grouped, placing his "immature" and "spawned-out" in "nonspawning" ("spawned-out" ovaries would have to be examined with a hand lens to eliminate those which still contained the yellowish, maturing ova in the follicles), and his "ripening" and "ripe" in "spawning," relatively few fish would be placed in different categories than those resulting from weighing the ovaries and the fish and plotting their coordinates on figure 6.

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[4] Only those ovaries in stage F which showed no evidence of previous spawning during the current year, as determined by the absence of remnants of ripe ova in the lumina, were used in the calculations.

NUMBER OF OVA SPAWNED

To estimate the number of ova produced at a single spawning by yellowfin tuna of different sizes, calculations were made for 11 fish over the size range 47.2 to 88.0 kg. (104 to 194 lbs.). (See table 6.) While estimations for a greater number of specimens would have been desirable, the labor involved in separating the ova from the follicles and the subsequent ova measurements precluded the study of additional material.

Table 6.—*Estimated number of ova produced at one spawning by yellowfin tuna*

Weight of fish	Calculated number of maturing ova
	Thousands
47 kg	2, 370
53 kg	3, 390
56 kg	4, 340
57 kg	5, 170
59 kg	3, 230
59 kg	6, 510
61 kg	3, 580
62 kg	5, 610
69 kg	6, 380
80 kg	6, 000
88 kg	8, 590

Ovaries were selected in which the most mature group of ova could be easily distinguished from ova being developed for subsequent spawnings and yet they were not sufficiently mature that any ova had been lost by spawning. Since it has been suggested that individual fish probably spawn more than once during a single breeding season, it is possible that subsequent spawnings would contain fewer ova; therefore, to make all estimations comparable, only ovaries in stage F which showed no evidence of previous spawning during the season were used. Accordingly, the estimates represent the number in the first of several possible spawnings. The method employed in calculating the number of ova was as follows: Ovaries from an individual fish were removed from the formalin preservative, and when sufficiently drained, they were weighed on a beam balance to the nearest 0.1 gram. A small sample of approximately 0.5 gram was removed from the ovaries and weighed on an analytical balance to the nearest 0.001 gram. The ova in the sample were teased out of the follicles, and measurements and counts were made of all ova composing the most mature group. The total number of ova in this group was calculated for each fish specimen by multiplying the ratio of the number of ova to the weight of the sample by the total weight of the preserved ovaries. Since the multiplier was in the order of 10,000, the estimate was recorded only to the nearest ten thousand ova.

The data shown in table 6 indicate that the number of ova produced at a single spawning increases with the size of the fish. This phenomenon has been demonstrated for many fishes, including the Volga-Caspian herrings, *Caspiolosa caspia*, *C. c. saposhnikovi*, *C. c. volgensis*, and *C. c. kesselri* (Kisselevitch 1923), the grunion, *Leuresthes tenius* (Clark 1925), the California barracuda, *Sphyraena argentea*, (Walford 1932), the California sardine, *Sardinops caerulea*, (Clark 1934), and the surf smelt, *Hypomesus pretiosus*, (Schaefer 1936). The relation between number of ova and size of fish for the yellowfin tuna is shown graphically in figure 7. Assuming the

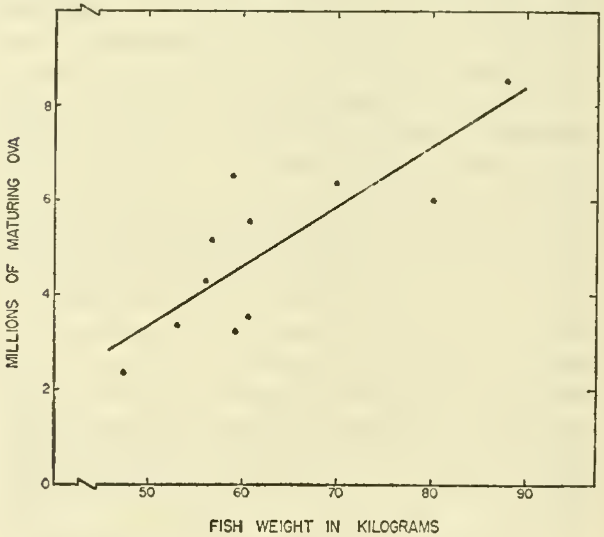

Figure 7.—Scatter diagram showing relation between the calculated number of ova produced for one spawning and the body weight of the fish.

relation to be linear, a straight line was fitted to the data by the method of least squares and is described by the equation

$$Y=125{,}200X-2{,}853{,}000,$$

where Y is number of maturing ova and X is fish weight in kilograms.

With 2 to 8 million ova produced by a spawning female in one of several possible spawnings a season, it is likely that a season's spawning of a small female exceeds 5 million ova and of a large female may be in the order of tens of millions.

SPAWNING SEASON

Until recently, the period over which spawning of the yellowfin tuna takes place in Hawaiian waters has been a matter of conjecture. There are no previous reports in the literature with regard to spawning of the species in this area. Commercial fishermen and local fish dealers had observed fish with enlarged gonads during the summer months, but could give no reasonably accurate information about the time of year these maturing ovaries occurred. It was not until 1949, when ovaries of yellowfin tuna first were sampled from landings of the longline fishery, that estimates of the onset and cessation of the spawning period were possible.

As pointed out previously, the ovary collections made during 1950 were continuous over the 12-month period. Furthermore, it has been shown that ovaries of yellowfin tuna from local waters pass through a maturing process which is consummated in spawning at some time during the 12-month interval. It remains, therefore, for us to determine the period during which spawning is most active and to establish its limits.

On the basis of the stages of maturity already described, the relative percentages of fish with ovaries in these various stages in each month give a good indication of the extent of development of the ovaries with respect to time of year. These percentages are presented in table 2, and show that fish with ovaries in the immature and intermediate stages were found in the samples only during the early months, January through April, and in the latter part of the calendar year, indicating that spawning did not occur in Hawaiian waters during the period mid-November through April. Beginning in May, fish with ovaries in stage F were present in the fishery. Unfortunately, the samples available during this period were few in number and, indeed, they may not give a true indication of all stages of sexual development represented in the fishery at that time. By June, however, all maturing stages with the exception of E were present in the samples, and during July and August most of the maturing stages were represented. The first spawned-out fish were taken in our collections in mid-October; yet, at that time the ovaries of more than half the fish sampled were in the maturing stages (E, F, and G). A single fish was found with ovaries in stage F that showed no indication of having spawned previously during the year. During the first week of November, a specimen with ovaries in stage G was taken; however, the ovaries of all other fish sampled were in either immature or spawned-out stages.

The data of table 2 may be summarized by combining stages A, B, and C to represent fish in nonspawning condition and by combining stages D through J to represent spawning fish. Fish with ovaries in stage K represent the spawned-out condition. The relative numbers of fish in each group are expressed as monthly percentages and are shown graphically in figure 8.

If our samples represent general spawning conditions, then from the data presented in table 2 and figure 8 it must be concluded that the spawning season occurred between mid-May and November.

To determine whether the increase in ovary size during spawning could be utilized to deliniate the spawning season, two methods of treatment were used: (1) A plot was made of the semimonthly ratios of ovary weight to fish weight (fig. 9); and (2) another plot (fig. 10) was made of the monthly percentages of fish in spawning condition as determined from the ovary-weight to fish-weight relation of figure 6. For the latter curve, all values which were excluded by the dashed lines representing two standard deviations from the regression for stage-A ovaries were considered to indicate fish in a spawning condition. This criterion agrees almost completely with the ova-diameter measurements which indicated only two nonspawning females with greatly enlarged ovaries—one taken in April and the other in November.

Both curves show that the spawning season extended from May to November. The curve (fig. 10) based on proportion of fish in spawning con-

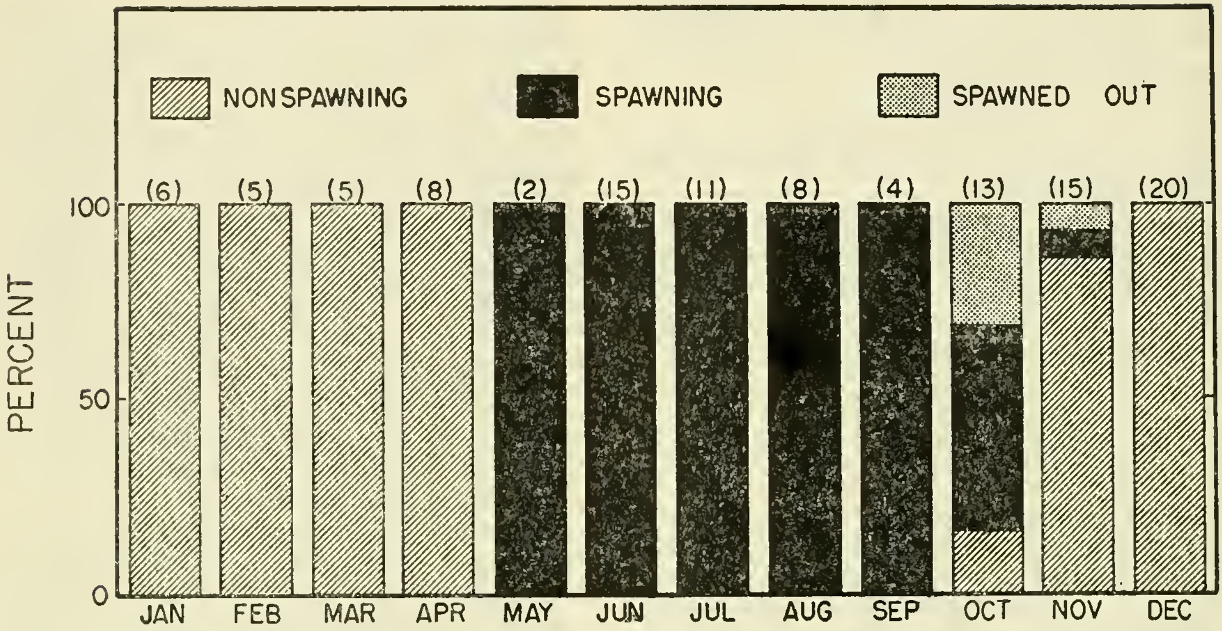

FIGURE 8.—Percentages of fish with ovaries in the nonspawning, spawning, and spawned-out conditions, by months. The number of fish included for each month is indicated at the top of each column.

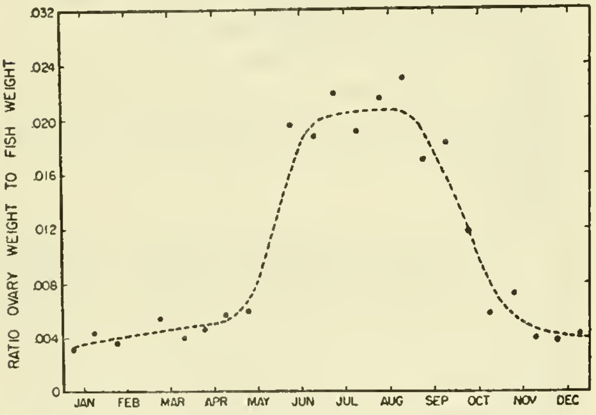

FIGURE 9.—The 1950 spawning season of yellowfin tuna as indicated by the mean ratios of ovary weight to body weight for all fish. The data are grouped into semimonthly periods.

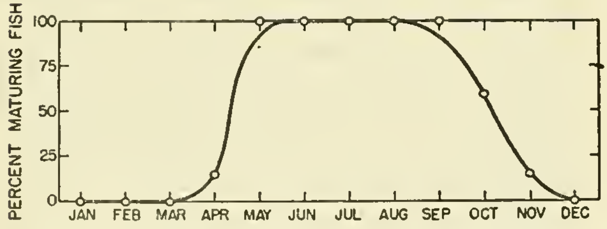

FIGURE 10.—The spawning season of yellowfin tuna represented by the percentages of maturing fish in each month, as determined by the ovary weight–fish weight regressions.

dition shows that no fish were in spawning condition from December through March, and that all were in that condition from May through September. The curve (fig. 9) based on ratios of ovary weight to fish weight, on the other hand, only shows that there was more spawning in the June to October period than in the rest of the year. Although interpretation of the ratios may make it possible to determine whether spawning involved all fish in the June to October period and none in the rest of the year, the regression method much more definitely establishes time and extent of spawning.

SPAWNING AND THE FISHING SEASON

The period of spawning and the peak of the fishing season so nearly coincide (fig. 11) that the fishery appears to be based on a spawning run. It should be remembered, however, that our use of the term "spawning fish" includes fish with well-developed ovaries that were not necessarily fully ripe for spawning. One fully ripe ovary was found among the samples taken. Fish that are actually spawning either do not take the hook or they migrate into deeper water outside the longlining grounds.

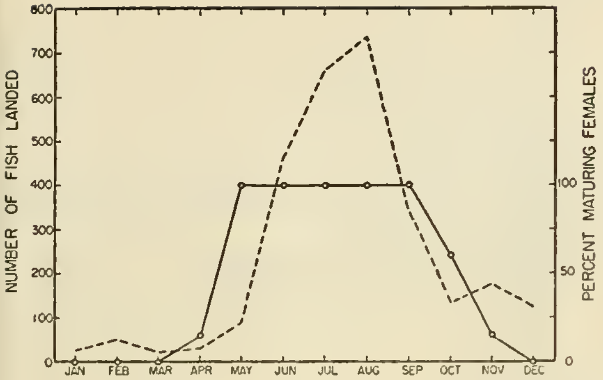

FIGURE 11.—Comparison of monthly yellowfin tuna landings for 1950 (– – – –) and the percentage of maturing females, as determined by the ovary weight-fish weight regressions (———).

SUMMARY

Ovaries from yellowfin tuna sampled from the longline catches landed at Honolulu during 1950 were used to determine the developmental changes that take place in the gonads during the breeding season, and data on the spawning of this species in Hawaii are presented.

It was found that several developmental groups of ova are present in the ovaries of individual fish during the breeding season. Based on diameter measurements of the most mature ova present, 11 arbitrary stages of maturity were established which trace the maturation of the ova from the immature stage through the spawning stage.

Several lines of evidence suggest that individual fish mature more than one group of ova and have several spawnings during the same season in Hawaiian waters. The number of ova produced in one spawning ranges from about 2,000,000 in small females to about 8,000,000 in large females.

Plotting ovary weight against fish weight yielded linear relations whereby the spawning condition of yellowfin tuna could be determined, thus providing a simple guide for distinguishing spawning from nonspawning fish without measuring ova.

The spawning period in Hawaiian waters during 1950 extended from about the middle of May to the end of October, and it was during this period that the best catches of yellowfin tuna were made in the longline fishery.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
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ESTIMATION OF GROWTH RATE IN ANIMALS BY MARKING EXPERIMENTS

By Milton J. Lindner

March 3, 1849

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ESTIMATION OF GROWTH RATE IN ANIMALS BY MARKING EXPERIMENTS

By MILTON J. LINDNER, *Fishery Research Biologist*

Effective action to conserve an animal resource must be based on such vital statistics as age composition of the stock and rates of mortality, replacement, and growth. In some species of animals, but unfortunately not in all, age and growth are indicated by the occurrence and spacing of rings on such hard parts as scales, bones, and shells. In studying shrimp (*Penaeus setiferus*) along the southern coast of the United States I found the problem of age determination particularly difficult, since no skeletal structures are carried over from one molt to another. Researchers studying other Crustacea report the same difficulty, with the result that growth of such important species as lobsters and crabs is imperfectly known.

The method for estimating growth described here can be used wherever growth follows geometric progression. It can be used in laboratory feeding experiments and with animals of unknown ages, and it is particularly useful when the age of animals cannot be ascertained by any other means. Although I stress the growth aspect in this paper, it is obvious that the method can be used also for determining age (only within the limits for which the technique is valid for growth) simply by plotting the results in the usual manner with size against time.

For equal time intervals Walford (1946) has demonstrated for many animals that growth, above the point of inflection on the curve of absolute growth, may be plotted as a straight line. This is accomplished by plotting the length at ages 1, 2, 3, 4 . . . on the X axis against length at ages 2, 3, 4, 5 . . . $n+1$ on the Y axis. The slope of this line is k. On the line, the length relations are such that:

$$L_n=\frac{1-k^n}{1-k}, L_{n+1}=L_1\,\frac{1-k^{n+1}}{1-k}\,k, = 1-\frac{L_1}{L_\infty},$$

$$\text{and } L_\infty=\frac{L_1}{1-k}.$$

L_∞ represents the ultimate length, which is also the point where this transformed growth line intersects the 45° line, or where $X=Y$.

Walford's transformation, which is based on the sizes of animals of known ages, can be modified to determine the growth rate of animals of unknown ages. This can be done because the time intervals are uniform or constant. As a consequence, if we take the lengths of a group of animals of unknown ages and of varying sizes on a certain day and measure these same animals again 1 year later, we shall have their respective lengths at age n and at age $n+1$ year. Plotting lengths n against $n+1$ will result in Walford's transformation for one time interval, in this instance, 1 year. If we should measure these same animals 2 years later and plot them in the same fashion (n against $n+2$), we should have a growth line representing the increment for 2-year intervals. From the relations between these lines we can arrive at the growth rate of an animal for any time interval we choose. The time interval, of course, must be constant.

A graphical representation of the relation between transformation lines obtained by plotting n against $n+1$, $n+2$, $n+3$, and so on, is shown in figure 1. Line A represents the transformed growth for one time interval, or Walford's transformation (n against $n+1$), line B for two time intervals (n against $n+2$), line C for three intervals (n against $n+3$) and so on.

In each instance, the length of the horizontal lines extended from L_2 to intersect line A, from L_3 to line B, from L_4 to line C, and so on, are equal. The length of each line is also equal to L_1. Consequently, if we know the sizes of a number of animals of different ages on a certain date and can measure these same animals (or representative samples of them) at successively equal later intervals of time, we can determine their growth line (Walford line) for the time interval chosen. An

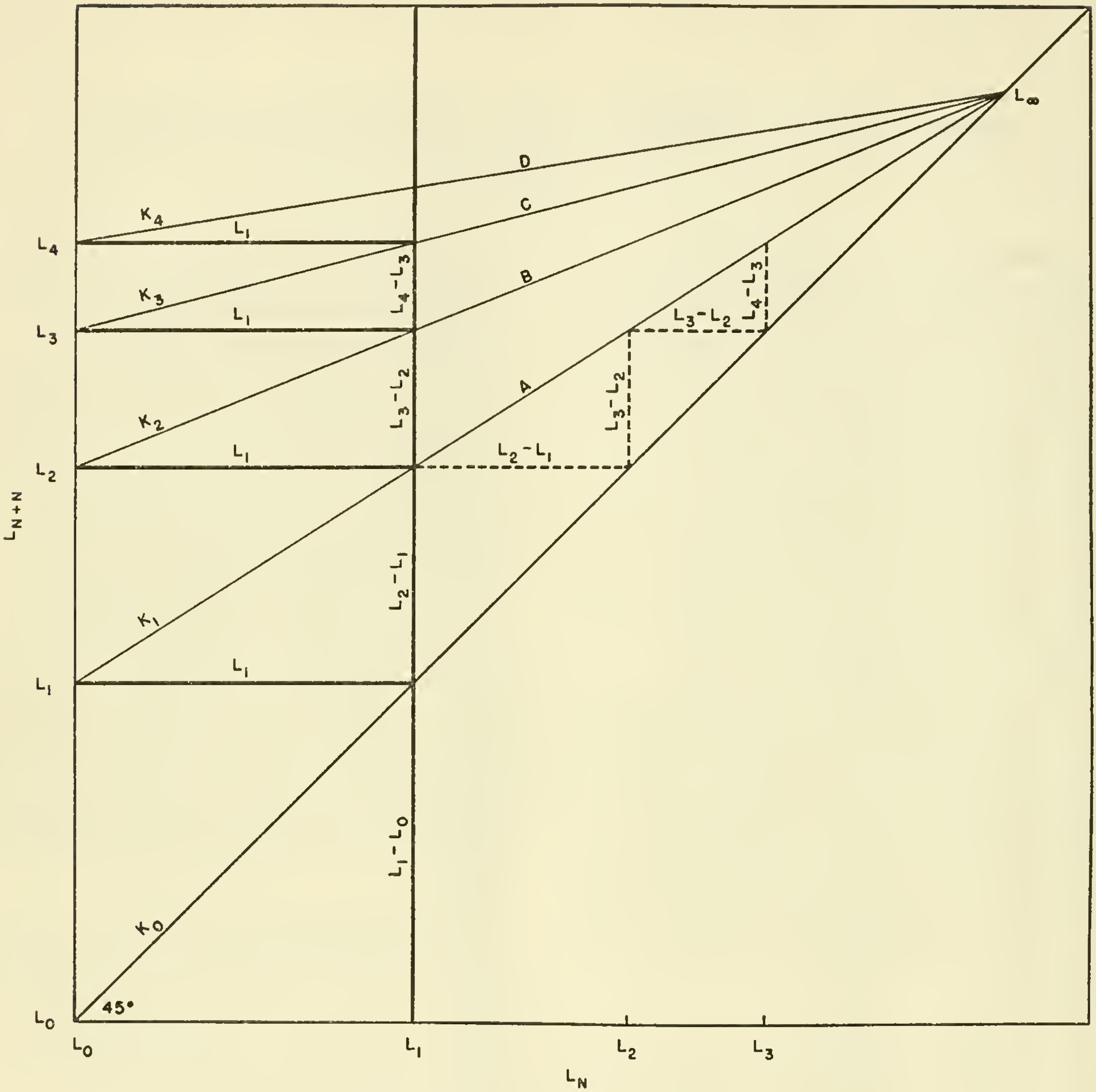

FIGURE 1.—*Relation between growth lines.*

estimate of L_1 can be obtained as just described, an estimate of L_∞ can be obtained from where the various lines intersect the 45° line drawn from zero, and k can be calculated from L_1 and L_∞.

The technique described is graphic. The same results can be obtained mathematically. The slopes of the various lines in figure 1 are

$$k_0=\frac{L_1-L_0}{L_1},\ k_1=\frac{L_2-L_1}{L_1},\ k_2=\frac{L_3-L_2}{L_1},$$

$$k_3=\frac{L_4-L_3}{L_1},\ k_4=\frac{L_5-L_4}{L_1},\ \ldots\ k_n=\frac{L_{n+1}-L_n}{L_1}.$$

Consequently $L_1=\dfrac{L_{n+1}-L_n}{k_n}$ . . . .(1)

But $L_n=L_1\dfrac{1-k^n}{1-k}$ and $L_{n+1}=L_1\dfrac{1-k^{n+1}}{1-k}$.

Subtracting L_n from L_{n+1} we obtain

$$L_1k^n(1-k)=(1-k)(L_{n+1}-L_n)$$

or $L_1=\dfrac{L_{n+1}-L_n}{k^n}$ . . . .(2)

But $L_1=\dfrac{L_{n+1}-L_n}{k_n}=\dfrac{L_{n+1}-L_n}{k^n}$; consequently $k_n=k^n$.

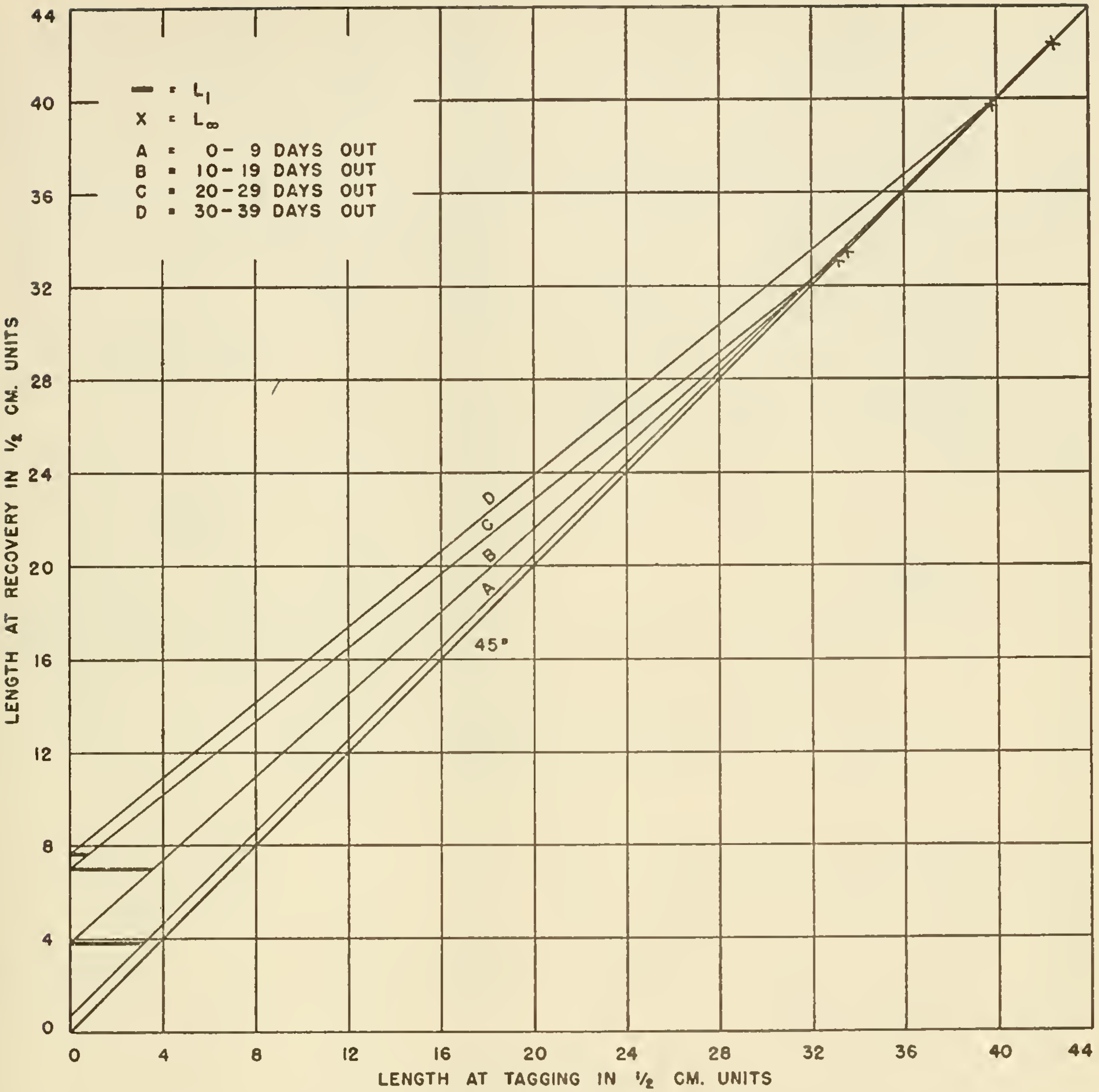

FIGURE 2.—Growth lines determined from marked shrimp, with estimates of L_1 and L_∞.

In Walford's transformation the two important points are L_∞ and L_1. These are obtained where $Y=X$ and where $X=0$, respectively.

L_∞ can be calculated readily from the fact that $Y=a+bX$ and when $Y=X$, also $Y=\frac{a}{1-b}=L_\infty$. (3)

Where L_1 is being obtained from two or more transformation lines, approximations can be reached by using formula 1.

When transformation lines can be obtained from two or more successive time intervals, approximations to L_∞ and L_1 can be obtained from their respective means.

As an example of this procedure, I am giving here the processes followed in obtaining a growth approximation from an experiment with marked shrimp.

As Walford (1946) has cautioned, a great many specimens are required for an accurate approximation to a growth line. The experiment I cite has very few specimens and cannot be regarded as representing growth in shrimp (*Penaeus setiferus*). I use it only to demonstrate the technique. As a matter of fact, because of the variability of the data I believe that, in an example such as this, results just as significantly accurate could be obtained by merely plotting the data, fitting the lines by eye, and estimating the L_1's and L_∞'s from the graph.

Between September 20 and 25, 1939, we measured in ½-cm. units and marked a number of shrimp in the Gulf of Mexico. We measured the shrimp again upon recapture.

I divided the returns (sexes combined) into four equal time intervals of 10 days each—0 to 9 days out, 10 to 19 days out, 20 to 29 days out, and 30 to 39 days out—and arranged the number of returns in tabular form with lengths at tagging against lengths at return. I fitted lines by least squares to these data, with X=length at tagging and Y=length at return. See tabulation following and figure 2.

Number of days out	Number of shrimp marked	Line formula	L_∞	L_1
0–9	314	$Y=0.678+0.984X$	42.38	3.22
10–19	72	$Y=3.850+\ .885X$	33.48	3.54
20–29	30	$Y=6.984+\ .789X$	33.10	0.78
30–39	35	$Y=7.600+\ .809X$	39.79	
Sum			106.37	7.54
Mean			35.46	2.51

In the tabulation, L_∞ for 0–9 days out was not used in calculating the sum or the mean L_∞ as it represents only an average of 5 days' growth. In using this technique I wish to caution against taking too short a time interval or too large a measuring unit. There is always the possibility under these circumstances that L_∞ will be either too large or too small. When the growth line tends to parallel the 45° line, L_∞ will be too large. When L_∞ tends to represent the larger individuals at time of marking, it generally will be too small. In this instance the tendency was to approximate the 45° line, probably making L_∞ too large.

In each instance, I calculated L_∞ from the constants in the line formula and from $L_\infty=\frac{a}{1-b}$. For example, for 0–9 days out $L_\infty=\frac{0.678}{1-0.984}=42.38$ ½-cm units or 211.9 mm.

I calculated L_1 from two successive lines and the formula $L_1=\frac{L_{n+1}-L_n}{k_n}$.

For example, L_1 calculated from the 0–9 and 10–19 day lines is $L_1=\frac{3.850-0.678}{0.984}=3.22$ ½-cm. units.

I obtained Walford's 10-day growth line from the mean L_∞ and the mean L_1 and from the formula $k=1-\frac{L_1}{L_\infty}$; $k=1-\frac{2.51}{35.46}=0.9292$.

Hence, Walford's line for 10-day intervals for this group of shrimp is $Y=2.51+0.9292X$.

However, in order to compare growth calculated in this fashion with monthly size distributions of the shrimp populations, I found it necessary to have a 30-day instead of a 10-day Walford line. In other words, I needed an L_3 instead of an L_1 line. This was obtained by

$$L_3=L_1\frac{1-k^3}{1-k}=2.51\frac{(1-0.9292^3)}{1-0.9292}=7.01;$$

$$k_3=1-\frac{L_3}{L_\infty}=1-\frac{7.01}{35.46}=0.8023.$$

Hence, for a 30-day Walford line in ½-cm units $Y=7.01+0.8023X$.

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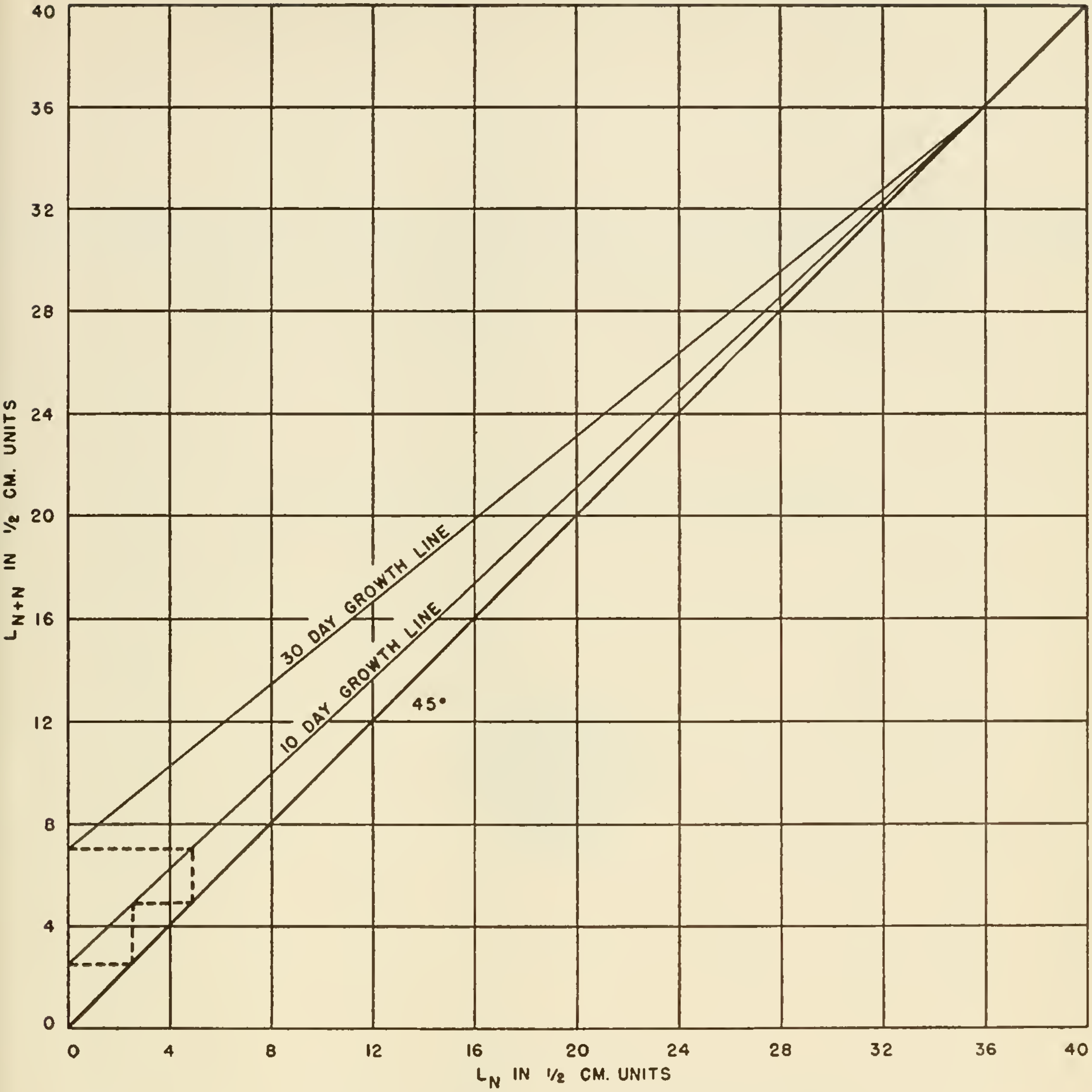

FIGURE 3.—Ten-day and thirty-day growth lines determined from mean estimates of L_1 and L_∞.

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STABILIZATION OF THE PHOSPHATE RATIO OF SEA WATER BY FREEZING

By Albert W. Collier and Kenneth T. Marvin

March 3, 1849

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OGICAL

STABILIZATION OF THE PHOSPHATE RATIO OF SEA WATER BY FREEZING

By **Albert W. Collier**, *Fishery Research Biologist*
and **Kenneth T. Marvin**, *Chemist*

It is the accepted practice in oceanographic investigations to make all chemical analyses, except salinity determinations, at sea. This is necessary because there has been no way in which samples could be stabilized for the relatively long period intervening between the collection of samples and the return to base. Only a limited number of analyses can be performed at sea, as a rolling, vibrating ship is not suitable for the delicate instruments required to make many of the chemical analyses. The chemists assigned to oceanographic investigations have thus been forced to make determinations under conditions unfavorable to producing the best quality or the greatest quantity of work.

Since the program of the Gulf Fishery Investigations of the United States Fish and Wildlife Service necessitated expansion of chemical investigation into the fields of organic chemistry and of biochemistry, it was essential that we find some method of overcoming the difficulties to making chemical analyses at sea. We desired to increase the precision and quality of work and to take advantage of the gain in productive manpower inherent in chemists working ashore, so as to make an intensive study of the phosphorus economy of the sea, reexamine the nitrate problem, and study the organic compounds present in sea water.

This paper reports the first of a series of experiments to test the stability of certain organic and inorganic complexes in sea water after the samples have been quick-frozen. The analysis for inorganic phosphorus is universally used in oceanography and marine biology and is very sensitive to changes in biological activity. Accordingly, we selected it as the first of a series for testing and reporting.

TECHNIQUES OF FREEZING AND ANALYSIS

Sea water was collected from Offat's Bayou, a small inlet on the bay side of Galveston Island, and from the open beach of the Gulf of Mexico near the laboratory. Normally, the waters of Offat's Bayou are richer in phosphate than are the waters of the Gulf of Mexico. The bottles found most satisfactory for this work were 4-ounce prescription bottles with molded plastic screw caps. They withstood the freezing well with only occasional breakage.

Freezing was accomplished by immersing the sample bottles in a bath of dry ice and ethyl alcohol. Preliminary tests demonstrated that ordinary refrigeration did not stabilize the materials, and that even freezing in the ice-tray section of an ordinary refrigerator was too slow. The dry-ice-and-alcohol bath made an easily portable arrangement, and froze the samples quickly enough to be effective.

Conditions aboard ship made certain modifications of this method necessary. Samples to be frozen were collected in glass culture tubes (25 x 200 millimeters) fitted with molded plastic screw caps. To speed the freezing of sea-water samples and to save time on shipboard, the sample tubes were prerinsed three times with distilled water and thoroughly drained in the shore laboratory before the ship sailed. Before the samples were put in the freezing bath the tubes were tightly sealed at the junction of cap and tube with plastic insulating tape. This prevented contamination by the freezing solution or by the water of the bath during thawing.

Freezing was done in a vat of 38 percent ethylene glycol held at an average temperature of −5° F. in a commercial quick-freeze cabinet installed for the purpose on the *Alaska*. The samples collected at one station were left in the freezing bath until the next station was reached, although they were well below 0° F. in less than 4 minutes. The samples were recorded according to their permanently affixed serial numbers.

The inorganic phosphorus was determined by the method described by Robinson and Thompson (1948) except that color intensity was measured with a Fisher AC electrophotometer. Our analyses were within the 10-percent limits of error given by Robinson and Thompson. All references to concentration of phosphorus are in terms of μ-gram atoms of phosphate phosphorus per liter.

EXPERIMENTS TESTING THE BEHAVIOR OF INORGANIC PHOSPHORUS IN SEA WATER

Experiment 1

Experiment 1 was set up to record any changes that occurred in the concentration of inorganic phosphorus in sea water left standing in sample bottles at room temperature. Such data were needed for comparison with those from the frozen samples.

Sea water was collected in Offat's Bayou and transported to the laboratory in a 5-gallon glass container. There it was filtered into a second glass container to remove gross particulate material, and from it 107 samples were siphoned into the prescription bottles. These samples were arranged in sets of 8, 9, or 10 bottles each, to be used as replicates for analysis at selected time intervals, and were placed on a table in the laboratory.

The initial phosphorus determinations were made after the water was filtered and before the first sample was drawn. The average value for each subsequent set of replicates was compared with the average of this initial set of eight. The sets comprising the series were analyzed consecutively at comparatively short intervals for the first 27 hours, and at longer intervals thereafter. The final analysis was made 29 days after the experiment was started. The results for the several time intervals, together with certain statistics pertaining to them, are shown in table 1.

The initial concentration was 2.54, but within 2 hours the next set gave a value of 2.58, to be followed by a drop to 2.45. This decline continued until the twenty-first hour when the concentration was 1.60. After this there were minor fluctuations around 2.00 for the remainder of the period. The "Student" *t* test was applied for comparing the mean of the initial set with the means of the subsequent sets, ending with the fifth hour.

The data for the first three time intervals were tested by the analysis of variance. The analysis was not extended beyond the fifth hour since the changes beyond that time were obviously significant. The means tested within the 5-hour period demonstrate heterogeneity, since *F* exceeds 32, which is significant at the 1-percent level.

TABLE 1.—*Changes in inorganic-phosphorus concentration of sea water occurring at room temperatures*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	8	2.54	0.092	0.1134
2 hrs	9	2.58	.067	.0746
3 hrs	10	2.45	.085	.0873
5 hrs	10	2.27	.048	.0496
21 hrs	10	1.60	----------	----------
27 hrs	10	1.68	----------	----------
2 days	10	2.02	----------	----------
3 days	10	2.20	----------	----------
17 days	10	2.04	----------	----------
21 days	10	1.93	----------	----------
29 days	10	2.20	----------	----------

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
2 hrs	+0.04	1.045	15
3 hrs	−0.09	*2.097	10
5 hrs	−0.27	**7.986	16

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	3	0.532	0.1773
Within sets	33	.180	.0055
Total	36	.712	----------

F=**32.24 between sets

Experiment 2

Experiment 2 was designed to test the rate of change of inorganic phosphorus at subzero temperatures. As in experiment 1, sea water was taken at Offat's Bayou and filtered at the laboratory to remove gross particulate material. Ten sets of samples were drawn, the first analyzed at once and the remaining nine frozen for later analysis. It required 15 minutes to draw and freeze each of the nine sets. The first was analyzed on the following day, the last on the forty-fifth day. The results are shown in table 2.

While only small differences developed between the means of the initial and the final sets, five means were different, according to the *t* test. These variations between time intervals, while slight, are reflected in an *F* value of 3.78, which is significant at the 1-percent level.

From the results of these first two experiments it became suspect that the 2-hour interval required to draw and freeze the 10 sets introduced a variable, in that changes in inorganic-phosphorus content were taking place even in that short interval. Subsequent experiments were designed to control this variable.

TABLE 2.—*Changes in inorganic-phosphorus concentration of sea water occurring at subzero temperatures*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	10	2.05	0.097	0.100
1 day	10	1.72	.181	.186
2 days	10	1.95	.097	.100
3 days	10	1.92	.225	.231
6 days	7	1.84	.172	.241
8 days	10	1.88	.162	.166
21 days	8	1.90	.141	.175
29 days	10	1.89	.090	.090
37 days	9	2.02	.140	.158
45 days	8	1.99	.155	.192

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
1 day	−0.33	**5.072	18
2 days	−.10	2.301	18
3 days	−.13	1.677	18
6 days	−.21	**3.179	15
8 days	−.17	*2.847	18
21 days	−.15	*2.667	16
29 days	−.18	**3.868	18
37 days	−.03	.509	17
45 days	−.06	1.046	16

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	9	0.777	0.086
Within sets	82	1.868	.023
Total	91	2.646	----------

F=**3.78 between sets

Experiment 3

Experiment 3 was designed, as were experiments 1 and 2, to measure the differences between rates of change in inorganic phosphorus stored at room temperature and at subzero temperatures. It was modified from these by the addition of inorganic and organic phosphorus, the former as potassium phosphate (dihydrogen) C. P., the latter as sodium glycerophosphate (Eastman). These were added to ensure a sufficient substrate of phosphorus to permit greater changes in concentration than could occur in phosphorus-deficient natural sea water.

The sea water for this experiment was taken from Galveston Beach. After adding the phosphorus, the mixture was filtered before drawing the samples. Altogether, 13 sets of samples were drawn, 5 to be kept at room temperature, 8 to be frozen. The results of these experiments are shown in tables 3 and 4.

In the 25 days during which the samples were held at room temperature, the concentration of inorganic phosphorus nearly doubled (table 3). As shown by the *t* test, each set of samples was significantly different from the initial set. The high values for the mean squares in the analysis of variance indicate the great differences which resulted between sets as compared with the differences within sets.

TABLE 3.—*Changes in inorganic-phosphorus concentration of sea water with added phosphorus, occurring at room temperature*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	19	5.83	0.1202	0.134
1 day	10	6.38	.148	.152
3 days	10	8.01	.357	.367
17 days	10	8.90	.226	.232
25 days	10	10.24	.232	.238

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
1 day	0.55	**11.193	27
3 days	2.18	**24.872	27
17 days	3.07	**48.975	27
25 days	4.41	**69.141	27

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	4	162.837	40.709
Within sets	54	2.528	.047
Total	58	165.362	----------

F=**869.85 between sets

By comparison, and in confirmation of the results shown in experiment 2, while the mean of the set held 61 days at subzero temperatures is not significantly different from that of the initial set, 4 of the 7 sets show differences with the *t* test (table 4). The analysis of variance also shows a possible significant difference between sets.

From these results it became increasingly evident that the time required to process the samples was introducing an uncontrolled variable, with changes in the ratio of inorganic to organic phosphorus being more rapid than had been suspected. The following experiment was designed to control this.

TABLE 4.—*Changes in inorganic-phosphorus concentration of sea water with added phosphorus, occurring at subzero temperatures*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	19	5.83	0.115	0.076
1 day	9	5.64	.219	.244
2 days	10	5.54	.268	.275
3 days	10	5.64	.334	.343
10 days	10	5.63	.400	.411
13 days	10	5.78	.187	.193
18 days	9	5.58	.156	.175
61 days	6	5.78	.172	.284

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
1 day	−0.19	**2.914	26
2 days	−.29	**4.057	27
3 days	−.19	*2.225	27
10 days	−.20	.016	27
13 days	−.05	.828	27
18 days	−.25	**4.762	26
61 days	−.05	.710	23

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	7	0.904	0.129
Within sets	75	4.368	.058
Total	82	5.272	----------

F=*2.220 between sets

Experiment 4

Experiment 4 was designed to appraise the effects of the delay inherent in drawing a large number of samples on the concentration of inorganic phosphorus. In this experiment, six sets of samples were drawn as rapidly as possible directly from Offat's Bayou. Filtering was eliminated to expedite the operation. In the initial set, the molybdate reagent was added to stabilize the samples, and the set was analyzed immediately on return to the laboratory. Subsequent samples, held at room temperature, were analyzed at the intervals shown in table 5.

The increases of 0.2 μ-gram atoms from 1.38 during the first 30 minutes and of 0.36 μ-gram atoms within the first 90 minutes, and the subsequent rise to 1.80 and decline to 1.68 μ-gram atoms, indicate how rapidly changes can take place at room temperature and explain, in part at least, the variations which developed in experiments 2 and 3. It is important to note that, while each set of samples was significantly different from the initial, as shown by the *t* test, and that the variations between sets in the analysis of variance was large in relation to the variance within sets, the standard deviations and the variance within sets were nominal. The importance of adequate stabilization or immediate analysis in determining the inorganic-phosphate ratio is here clearly demonstrated.

TABLE 5.—*Changes in inorganic-phosphorus concentration of sea water occurring at room temperature*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	9	1.38	0.067	0.075
30 min	5	1.60	.122	.252
90 min	7	1.74	.098	.137
3 hrs	8	1.80	.160	.198
4 hrs	9	1.78	.083	.093
5 hrs	9	1.68	.097	.109

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
30 min	0.22	**4.422	12
90 min	.36	**8.774	14
3 hrs	.42	**7.209	15
4 hrs	.40	**11.239	16
5 hrs	.30	**7.635	16

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	5	1.067	0.213
Within sets	41	.464	.011
Total	46	1.531	----------

F=**18.85 between sets

Experiments 5 and 6

Experiment 5 was designed to obtain more nearly exact information on the effect of freezing on the changes in the concentration of inorganic phosphorus by minimizing the delay inherent in drawing and freezing a large number of samples. As in experiment 4, samples were drawn from Offat's Bayou as rapidly as possible and without filtering. The samples were frozen immediately. Again, the molybdate reagent was added to the initial set, which was analyzed immediately on return to the laboratory. In each, the molybdate reagent was added to the sample as it was placed in the water bath so as to minimize changes which might take place in the period of thawing.

In this experiment, the first set of samples was analyzed 90 minutes after freezing, the last set 4¼ hours later (table 6). With this technique, no differences are evident either in the *t* test or in the *F* value of the analysis of variance.

TABLE 6.—*Changes in inorganic-phosphorus concentration of sea water occurring at subzero temperatures*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	9	2.90	0.492	0.551
1½ hrs	8	2.65	.093	.114
3¼ hrs	9	2.70	.206	.231
4¾ hrs	10	2.95	.530	.544
5¾ hrs	11	2.80	.417	.399

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
1½ hrs	−0.25	1.409	15
8½ hrs	−.20	1.124	16
4¾ hrs	+.05	.212	17
5¾ hrs	−.10	.492	18

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	4	0.583	0.146
Within sets	42	6.605	.157
Total	46	7.188	----------

$F < 1$ between sets

The same techniques were employed in experiment 6 as in experiment 5, but the samples were held for a longer period of time, as shown in table 7. Here, again, the rapid freezing techniques minimized changes during the period of collection, so that no significant changes in the concentrations of inorganic phosphorus were evidenced in the *t* test. The difference shown in the *F* test of the analysis of variance, being greater within than between sets, is probably due to particulate material, since these samples were not filtered. The variance between sets is at a minimum. From these experiments, it is apparent that rapid freezing and holding of samples at subzero temperatures effectively stabilizes the inorganic-phosphate ratio, so permits of analysis even weeks after collection with greater assurance of accuracy than if any delay is encountered between collection and analysis.

TABLE 7.—*Changes in inorganic-phosphorus concentration of sea water occurring at subzero temperatures*

A. VALUES IN μ-GRAM ATOMS OF PO_4-P PER LITER

Time interval	Number in set	Mean	Standard deviation	Fiducial limits ($t_{.01}$)
Initial	7	2.26	0.127	0.178
2 hrs	10	2.24	.196	.201
3¼ hrs	7	2.29	.069	.097
1 day	10	2.24	.237	.243
3 days	10	2.27	.275	.283
7 days	9	2.27	.206	.231

B. COMPARISON OF MEAN OF INITIAL SET WITH MEANS OF SUBSEQUENT SETS

Time interval	Difference between means	Value of *t*	Degrees of freedom
2 hrs	−0.02	0.202	15
3¼ hrs	+.03	.527	12
1 day	−.02	.173	15
3 days	+.01	.115	15
7 days	+.01	.108	14

C. ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sets	5	0.014	0.003
Within sets	47	1.995	.042
Total	52	2.009	----------

$F < 1$ between sets

CONCLUSIONS

Robinson and Thompson (1948) stated that determination of the inorganic-phosphorus content of sea water must be made as soon as possible after collection of the samples. This is borne out by the results of this study which give definite proof that changes can take place within 30 minutes. The data shown in table 5 demonstrate this.

It is also clearly demonstrated that these same changes can be completely arrested for prolonged periods by quick-freezing, and that this method of stabilization has sufficient reliability for general adoption.

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1948. The determination of phosphates in sea water. Jour. Marine Research 7 : 33–41.

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FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

PHOSPHORUS EXCHANGE IN MARINE PHYTOPLANKTON

By Theodore R. Rice

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PHOSPHORUS EXCHANGE IN MARINE PHYTOPLANKTON

By Theodore R. Rice, *Fishery Research Biologist*

The labeling of planktonic algae with radioactive phosphorus was investigated as one phase of a study of the food of filter-feeding invertebrates. The phytoplankton first had to be grown under conditions that would result in the cells absorbing and retaining large quantities of active phosphorus before it could be used as labeled food. This required that the processes of phosphorus exchange in phytoplankton be analyzed.

The relative abundance of phosphorus has been known to be a factor limiting the growth of phytoplankton in the sea since the time of Brandt (1899, 1902). Studies in the laboratory with pure cultures, as well as correlations resulting from work in the field, have proved phosphorus to be of critical importance. Its abundance in natural bodies of water previous to rapid increases in population sizes and its seasonal depletion with an increase of phytoplankton have been shown many times.

A decrease in the phosphorus concentration of the medium following an increase in the phytoplankton population has been relatively easy to demonstrate in the laboratory. Detection of phosphorus exchange was not possible until tracer techniques for active phosphorus were developed. By using a culture medium containing a mixture of radioactive and nonradioactive phosphorus, a measurement of phosphorus exchange is possible. The normal movement of phosphorus can be traced by following the movement of radioactive phosphorus, since it is generally accepted that cells cannot distinguish between the two isotopes of phosphorus and that isotopic effects can be disregarded. Furthermore, the addition of small amounts of radioactive phosphorus, in these studies, has not changed the physiology of the cells through radiation, nor the rate of uptake of phosphorus by them.

Using radioactive phosphorus, Gest and Kamen (1948) and Goldberg, Walker, and Whisenand (1951) have demonstrated that phosphorus is exchanged by planktonic algae. In both of these investigations, exchange was tested for only short intervals of time by either centrifuging or filter-washing the cells containing radioactive phosphorus. The appearance of radioactive phosphorus in the washings demonstrated exchange. Although filter-washing also has been used in this investigation to determine factors influencing exchange, emphasis has been placed on measuring exchange over longer periods of time while the cells were maintained under various environmental conditions.

MATERIALS AND METHODS

CULTURE MEDIUM

The addition of nutrients to natural sea water is still apparently the best method of preparing culture medium for marine planktonic algae. One disadvantage of this method is that precipitates often form when the enriched sea water is autoclaved. It was important that no precipitates form in the medium used in these experiments, since the radioactive phosphorus must be contained either in the cells or in the medium. Sea water enriched with Miquel's solutions, as modified by Ketchum and Redfield (1938), was used since *Nitzschia closterium* grows well in this medium. It was found that their solutions A and B caused precipitates to form when added to sea water and autoclaved. By adding iron as $Fe(NH_4)(SO_4)_2$ instead of as $FeCl_3$ in solution B, and by removing the phosphate compound from solution B and adding it as solution C, the formation of precipitates was avoided. The same concentration of phosphorus, 56 μgAP/L added as KH_2PO_4 instead of as $Na_2HPO_4 \cdot 12H_2O$, was used to prepare solution C. The important change is that solution C was not added until after the sea water containing solution A and the modified solution B had been autoclaved and allowed to cool. If solution C was added to the

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Note.—This study was part of a project carried on under a cooperative agreement between the United States Fish and Wildlife Service and the United States Atomic Energy Commission.

autoclaved sea water before it had cooled completely, precipitates still formed.

The three solutions used in the preparation of this culture medium were—

Solution A	KNO_3	20.2 grams.
	Distilled water	To make 100 cubic centimeters of solution.
Solution B	$MgSO_4$	4 grams.
	$CaCl_2$	4 grams.
	$Fe(NH_4)(SO_4)_2$	1 gram.
	HCl (conc.)	2 cc.
	Distilled water	To make 100 cc. of solution.
Solution C	KH_2PO_4	1.53 grams.
	Distilled water	To make 100 cc. of solution.

Particulate matter was first removed from the sea water by filtering it through cotton. Then, 0.55 cc. of solution A and 0.50 cc. of solution B were added to each liter of sea water. This medium was autoclaved and, after cooling completely, 0.50 cc. of solution C, which had been autoclaved separately, was added aseptically.

CULTURE PROCEDURE

Nitzschia closterium was isolated into pure culture and used in these experiments. It was maintained in pure culture on agar containing 2 percent glucose and 0.5 percent peptone in addition to Miquel's inorganic nutrients. Tests for purity were not made on cultures during or after the experiments since sterile techniques and inorganic media were used and since most experiments were completed within a short period of time.

The cultures were grown in a refrigerated cabinet (fig. 1) at a temperature of 20°±2° C. The cabinet was equipped with adjustable wooden shelves to each of which six 40-watt daylight fluorescent lights, spaced 2 inches apart, were attached. Approximately 2 inches above the lights were glass shelves upon which the cultures were placed.

PHOSPHORUS MEASUREMENTS

The radioactive phosphorus used in these experiments came from Oak Ridge National Laboratory.[1] Activity was determined by means of a conventional dip-type Geiger-Müller counting tube connected with a scaler-of-64 circuit. The geometry was constant, and corrections for decay and coincidence loss were made. The radioactive phosphorus was standardized by comparison with a simulated standard of known microcurie strength. Inorganic-phosphorus concentrations were determined by the Atkins-Deniges molybdate method as modified by Wattenberg (1937). Salt-error corrections were made and algal cells were removed by filtering before making determinations. The intensity of the blue color was measured with a Klett-Summerson photoelectric colorimeter which had been standardized with solutions of known phosphorus content. Klett filter No. 66 and a 4.5 x 2.5 centimeter cell were used. Since the intensity of the blue color changes with time, determinations were made approximately 10 minutes after the addition of reagents. The concentration of phosphorus is expressed as microgram atoms of phosphate phosphorus per liter (μgAP/L) as recommended by the International Association of Physical Oceanography (Sverdrup, et al. 1942, table 34).

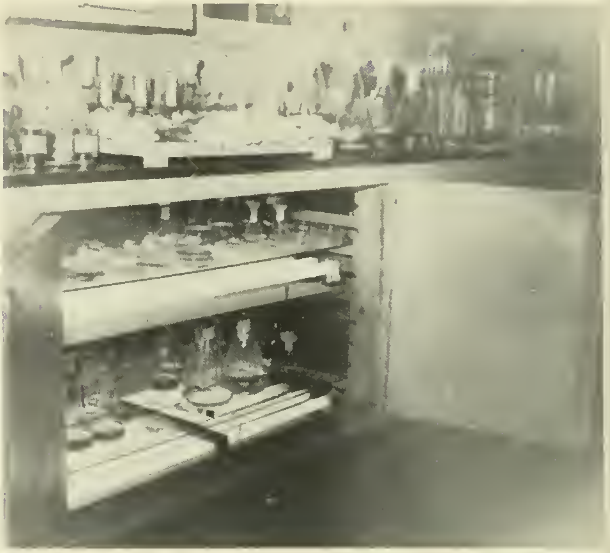

FIGURE 1.—Culture cabinet showing illumination of cultures.

DETERMINATION OF POPULATION SIZE

The number of cells per liter was determined by removing approximately 5 cc. of medium after vigorously shaking the culture to distribute the cells evenly throughout the medium. The average of two cell counts, made with an improved Neubauer haemocytometer, was taken as the population size. A careful check has shown that this method is very accurate for determining unialgal population sizes, the accuracy agreeing favorably with that found by other investigators (Pearsall and Loose 1937, Pratt 1940, and Winokur 1948).

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[1] Supplied on authorization from the Isotopes Division, United States Atomic Energy Commission.

PREPARATION OF FILTERS

A stainless-steel filter (fig. 2), which could be taken apart for the insertion of specially cut Whatman No. 42 filter paper, was used with a vacuum pump. The barium-sulfate precipitate was formed by heating 15 cc. of one-fifth normal H_2SO_4 and adding 0.6 cc. of normal $BaCl_2$. The precipitate was filtered onto the filter paper and rinsed with distilled water before filtrations were made.

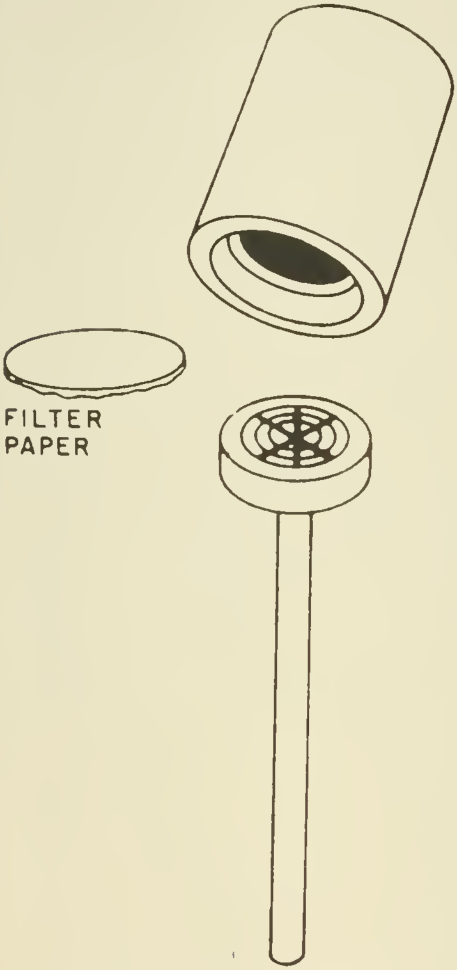

Figure 2.—Stainless-steel filter.

FRACTIONATION OF CELLS

The cells were centrifuged from the culture medium and extracted in the cold with 10 cc. of cold 10-percent trichloracetic acid (TCA) for about 1 hour. After centrifuging, extraction was repeated with a new volume of TCA. The TCA-insoluble residue was dissolved in HNO_3 and diluted with distilled water for counting. The TCA-soluble fraction was neutralized to phenolphthalein with NaOH and the inorganic phosphorus fraction was precipitated with 10-percent $CaCl_2$ in saturated $CaOH_2$. The precipitate, after centrifuging, was dissolved in a small amount of dilute HCl, made to volume with distilled water, and the radioactive disintegrations were counted. The supernatent was also made to volume with distilled water and counted. Thus the radioactive-phosphorus content of the inorganic phosphorus, the TCA-insoluble phosphorus (considered as protein-bound phosphorus), and the TCA-soluble organic phosphorus (ester phosphorus) were measured. The protein-bound phosphorus and the ester phosphorus were always combined and reported as the organic fraction.

EXPERIMENTS

PHOSPHORUS ABSORPTION

Phosphorus in culture medium containing dividing cells can be reduced below a concentration detectable with the colorimetric method of analysis if no other factor limits cell division. Consequently, it has been assumed that phosphorus completely disappears from the medium. By using radioactive phosphorus, the reduction of phosphorus in the culture medium can also be determined, provided no exchange of phosphorus occurs between the cells and the medium. To accomplish this requires only that a known amount of radioactive phosphorus be added to medium containing nonradioactive phosphorus prior to the addition of cells. Since the cells cannot distinguish between these two isotopes, the same percentage of each should be absorbed in any period of time. Thus, measurements of the radioactive phosphorus absorbed can be converted to represent inorganic phosphorus absorbed, since the initial ratio of the two is known.

To compare the absorption curves of phosphorus as determined with radioactivity measurements and with colorimetric analysis, culture medium was prepared with enough radioactive phosphorus to give 11,000 counts per minute per 25 cc. of medium and an inorganic phosphorus concentration of 44 μgAP/L. *Nitzschia* cells were added to this medium in sufficient quantity to give a population of 18.5 × 10^7 cells per liter and the culture was placed in the culture cabinet in the light. Counts for the radioactive phosphorus content of cells and colorimetric analysis for the inorganic-phosphorus content of the medium were made periodically. This colorimetric analysis also included the radioactive phosphorus in the medium, but there was such a small number of radioactive atoms that little, if any, change was caused by their presence or absence.

In figure 3, the amounts of radioactive and nonradioactive, or inorganic, phosphorus absorbed by the cells are shown. Since both radioactive and inorganic phosphorus are plotted on the vertical scale so that a certain percentage of one is equal to the same percentage of the other, the determinations for radioactive phosphorus also represent microgram-atoms of phosphorus. The cells continued to absorb phosphorus from the medium until it was reduced below a concentration detectable with the colorimetric method. However, radioactive determinations for phosphorus made at the end of this experiment showed that a trace of phosphorus still remained in the medium. This may be due to radioactive determinations being many times more sensitive than colorimetric determinations. It is believed that contamination can be ruled out. The author suggests that this trace of radioactive phosphorus in the medium is due to exchange from the cells.

From the two curves in figure 3 it can be seen that at first the absorption of radioactive phosphorus by the cells was greater than absorption determined by the decrease of inorganic phosphorus in the medium. This difference must be the result of exchange or of errors in measurement

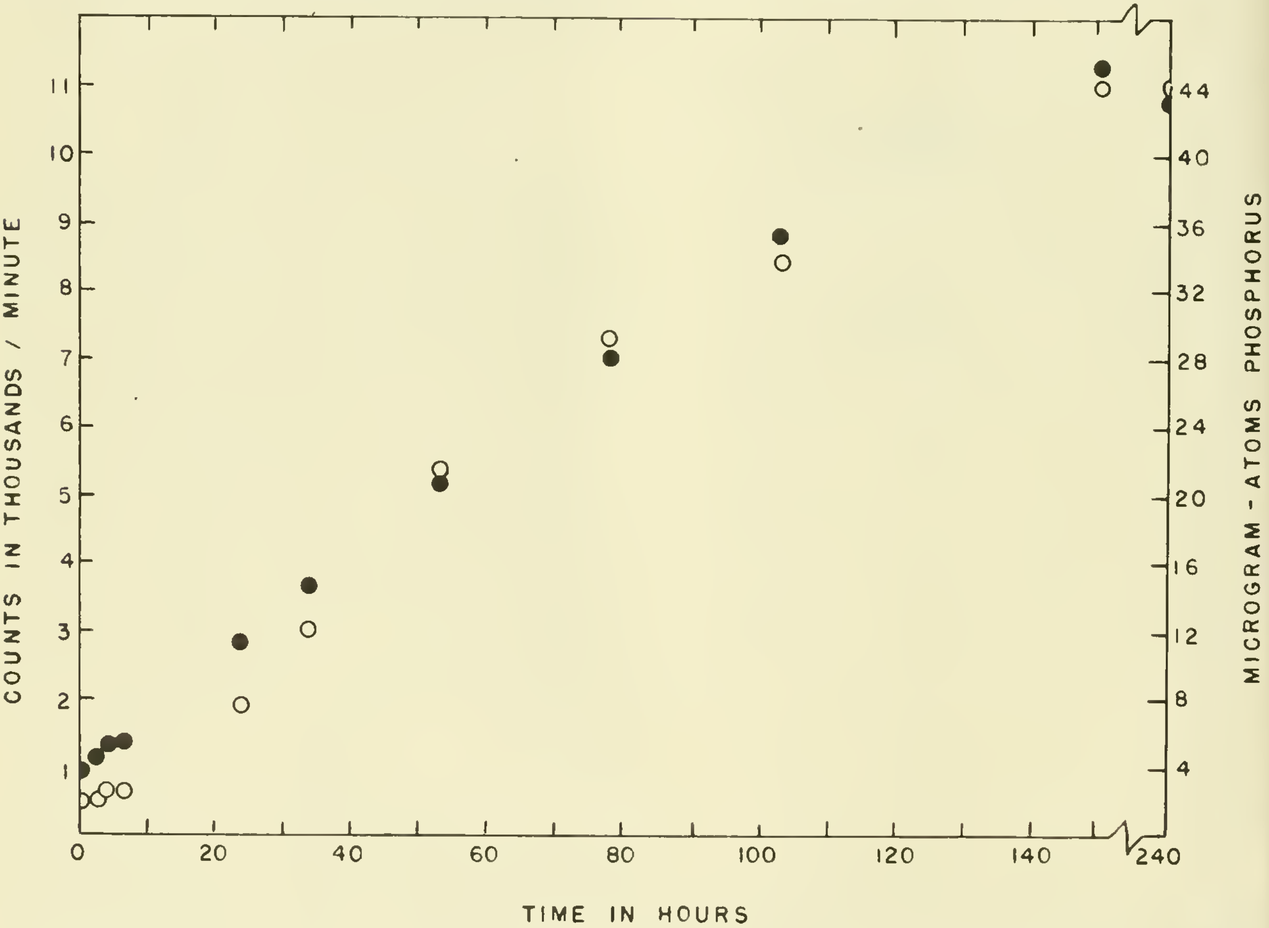

FIGURE 3.—Phosphorus absorption by *Nitzschia* cells as determined by both colorimetric and radioactivity measurements. Circles show amounts of inorganic phosphorus measured colorimetrically; dots show amounts of inorganic phosphorus from radioactivity observations.

or of a combination of the two. When exchange occurs, the specific activity, or ratio of radioactive to total phosphorus atoms, of the medium is changed. In this experiment only nonradioactive phosphorus could initially be exchanged from the cells since the cells had previously grown in medium containing only nonradioactive phosphorus. That the observed differences in the two curves could have been caused by exchange seems improbable, when the accuracy of the colorimetric method is considered. With this method small changes cannot accurately be determined. This is especially so when the medium contains large amounts of phosphorus requiring dilution to obtain satisfactory color intensities for measurement.

Even if all the difference between the two absorption curves could be attributed to exchange, which it cannot, the total amount of phosphorus exchanged would still be very small. From this experiment it can be concluded that, since the metabolic need for phosphorus by dividing cells is so great and the errors of the colorimetric method for measuring phosphorus are so large, any movement of phosphorus due to exchange cannot be detected with a reasonable degree of accuracy.

CONDITIONS AFFECTING PHOSPHORUS EXCHANGE BY CELLS WHEN FILTER-WASHED

Another way to detect exchange is to incorporate radioactive phosphorus into the cells before placing them in a medium which is continually renewed and which contains only nonradioactive phosphorus. If an exchange of phosphorus occurs, the radioactive phosphorus leaving the cells is removed before it can be reabsorbed by the cells. The appearance of radioactive phosphorus in the medium would indicate that phosphorus was being exchanged between cells and medium. Since the washing medium in these experiments contained the same concentration of nonradioactive phosphorus as the medium in which the cells had been growing, no differentiation could have been made between phosphorus originally in the washing medium or in the cells without the use of radioactive phosphorus.

In experiments conducted by Gest and Kamen (1948) on exchange by fresh-water algae, washings were made by centrifuging the cells containing radioactive phosphorus from the medium, decanting the medium, resuspending the cells in new medium, and repeating the process several times. This method was first used as a means of washing in these investigations, but it was later found that filter-washing was more suitable. Goldberg, et al. (1951) found that 50 percent of the radioactive phosphorus in the diatom *Asterionella japonica* is lost when the organism is washed while suspended on a filter. However, it will be shown that several factors may influence the amount of phosphorus exchanged from phytoplankton when filter-washed.

In the following experiments, *Nitzschia* cells in two different physiological states, nondeficient and phosphate-deficient, were used to follow phosphorus exchange. The nondeficient cells were grown in a north window in culture medium containing phosphorus, while the phosphate-deficient cells were grown for several days in the culture cabinet in medium containing no added phosphorus, following methods developed by Ketchum (1939b). The deficient cells continue to divide in the absence of phosphorus in the medium until the phosphorus in each cell is greatly reduced and a condition is reached where further division without phosphorus is impossible.

Exchange by nondeficient cells

The required number of cells were centrifuged from stock culture medium containing phosphorus. These cells were then resuspended in new culture medium and divided into two equal cultures. To one culture enough radioactive and nonactive phosphorus was added to give a concentration of 45.5 μgAP/L, and enough to give 1,137.5 μgAP/L was added to the remaining culture. To each culture, radioactive phosphorus was added in sufficient amounts to give a specific activity of 0.1624 μc/μgAP. Both cultures were placed in the culture cabinet in a constant source of light for 20 hours. During this time the cells took up phosphorus and became radioactive. At the end of 20 hours the cells from 50 cc. of each of these cultures were filtered by means of a $BaSO_4$ filter, and a radioactive count was made on them to determine the total radioactive phosphorus absorbed. To measure the loss of phosphorus, cells from another 50-cc. portion were then filtered and washed five times with 50-cc. portions of culture medium containing the same concentration of phosphorus as the medium in which these cells had been growing but to which no radioactive phosphorus had been added.

The 45.5 and 1,137.5 μgAP/L in these experiments will be referred to as low and high phosphorus concentrations. It is realized that the 45.5 μgAP/L is not a low concentration when compared with concentrations occurring in nature. However, the quantity of phosphorus available per cell is more important than the concentration per unit volume of medium. Since some populations of cells used are often many times greater than those ordinarily occurring in nature, the conditions in these cultures with the low concentrations may after all be very similar to natural conditions.

In all filter-washing experiments, the activity in the washings plus the activity still remaining in the cells after washing always amounted to at least 90 percent of the total activity contained in the same quantity of cells before washing. Thus, never more than 10 percent of the radioactive phosphorus was unaccounted for even though six different activity readings were made in the washing procedure.

Although the medium with the high phosphorus concentration contained 25 times more phosphorus than that of the low concentration, it also contained 25 times more radioactive phosphorus, specific activity being the same in both cultures. Like amounts of radioactive phosphorus absorbed or exchanged in either culture would therefore represent the same amount of phosphorus.

Loss of radioactive phosphorus to the medium showed that nondeficient cells grown in both the low and high phosphorus concentrations exchanged phosphorus with the medium when filter-washed (table 1). The cells grown in the high concentration not only absorbed more phosphorus from the medium in which they were grown but also exchanged more phosphorus with the medium when filter-washed. Ketchum (1939 a) has previously shown that *Nitzschia* cells absorb more phosphorus when grown in medium containing high phosphorus concentrations. Since the amount of phosphorus entering the cells is proportional to the concentration in the medium, it necessarily follows that any phosphorus entering the cells in excess of that which the cells can convert into the organic state, will remain in the inorganic state. This may explain the observation that, when other conditions are similar, the concentration of phosphorus in the medium in which cells are grown controls the amount of phosphorus in the cells available for exchange.

TABLE 1.—*Exchange by nondeficient cells grown in low and high phosphorus concentrations for 20 hours before filter-washing*

[Initial cell count was 46×10^7 cells per liter. Specific activity was 0.1624 μc/μgAP in both media]

Medium	Activity in cells from 50 cc. of medium in counts per minute	Activity lost by cells from 50 cc. of medium in counts per minute	Percentage exchanged
Low concentration (45.5 μgAP/L)	8,730	2,672	30.6
High concentration (1,137.5 μgAP/L)	185,100	171,670	92.7

Exchange by phosphate-deficient cells

Ketchum (1939 b) has shown that phosphate-deficient cells contain only a small fraction of the phosphorus found in nondeficient cells, and that more phosphorus is absorbed by deficient cells when again placed in medium containing phosphorus. Since the physiology of phosphate-deficient cells must be different from that of nondeficient cells, the amount of phosphorus exchanged by this type of cell when filter-washed was tested. The effects of low and high phosphorus concentrations on the amount of phosphorus exchanged was also determined.

The phosphate-deficient cells used in the experiment were prepared by suspending cells in medium to which no phosphorus had been added. After placing the culture in the cabinet in the light for 3 days, the population had increased from 45×10^7 to 82×10^7 cells per liter. Since the culture medium contained only a trace of phosphorus, the increase in the number of cells probably had reduced the amount of phosphorus within each cell to a point where further division was impossible. From this culture the cells were centrifuged, resuspended in medium containing radioactive phosphorus, and then filter-washed as described for the nondeficient cells.

Phosphate-deficient cells grown in the higher concentration of phosphorus absorbed more phosphorus than those grown in the lower concentration (table 2). Those grown in the higher concentration also lost a larger percentage of phosphorus when filter-washed. Thus, the phosphorus concentration of the medium in which the cells are grown controls the amount of phosphorus entering and exchanged by the phosphate-deficient cells, the same as for the nondeficient cells.

Comparison with the nondeficient cells of the preceding experiment (table 1) shows that phosphate-deficient cells grown in low concentrations of phosphorus absorbed more phosphorus than nondeficient cells grown in a similar concentration of phosphorus. Since the initial population sizes were approximately the same in this and the previous experiment, it can be assumed that the metabolic rate of the phosphate-deficient cells was higher than that of the nondeficient cells. Also, less phosphorus was exchanged by deficient cells when filter-washed even though they had absorbed more phosphorus. This was probably due to more of the phosphorus taken into the cells during this period of time being converted into the organic state.

Table 2.—*Exchange by phosphate-deficient cells grown in low and high phosphorus concentrations for 20 hours before filter-washing*

[Initial cell count was 45 × 10^7 cells per liter. Specific activity was 0.3538 μc/μgA P in both media]

Medium	Activity in cells from 50 cc. of medium in counts per minute	Activity lost by cells from 50 cc. of medium in counts per minute	Percentage exchanged
Low concentration (45.5 μgA P/L)	40,850	2,094	5.1
High concentration (1,137.5 μgA P/L)	399,375	101,604	25.4

Effect of exposure time on exchange

The smaller amounts of phosphorus exchanged by phosphate-deficient cells as compared with that exchanged by nondeficient cells in the previous experiment was due to an altered physiological condition. This difference in phosphorus exchange in the two different types of cells was expressed as the percent of the total radioactive phosphorus contained in the cells. Even though exchange between cells in the same physiological condition and the medium remains constant it would appear to decrease with time if expressed as a percent of the total radioactive phosphorus in the cells. This would be due to the amount of labeled phosphorus in the nonexchangeable fraction increasing during a longer growing period. This experiment only demonstrates the effect of time upon the amount of phosphorus exchanged when computed in the above manner and emphasizes the importance of considering the conditions of the experiment when exchange is expressed as a percent of total radioactive phosphorus.

The cells were taken from a culture similar to that used in the previous experiment with nondeficient cells. The cells were suspended in two cultures, the one with a low and the other with a high phosphorus concentration, and grown for 7 days in the culture cabinet in the light. The initial population of cells in these cultures was 10 × 10^7 cells per liter, a much smaller number of cells than was used in the previous experiments. This smaller initial population was used in order that the cells could continue to divide and convert inorganic phosphorus into organic-phosphorus compounds. After 7 days in the culture cabinet, the cells were filter-washed as in the two previous experiments.

The cells grown in the high concentration of phosphorus absorbed more phosphorus than those grown in the low concentration, as in the previous experiments (table 3). Similarly, the cells grown in the high concentration of phosphorus exchanged more phosphorus with the medium when filter-washed. Since the cells used in this experiment came from the same type of culture as those cells used in the first of these filter-washing experiments, a comparison of the results is possible. As would be expected, more radioactive phosphorus was absorbed by the cells during the 7-day period than by the cells grown for only 20 hours. Since more radioactive phosphorus entered the cells during this longer period, more was converted into organic compounds. Consequently, when filter-washed, a smaller percent of radioactive phosphorus was lost by the cells.

Table 3.—*Exchange by nondeficient cells grown in low and high phosphorus concentrations for 7 days prior to filter-washing*

[Exposure to radioactive phosphorus was also for the 7 days. Initial cell count was 10 × 10^7 cells per liter. Specific activity was 0.2923 μc/μgA P in both media]

Medium	Activity in cells from 50 cc. of medium in counts per minute	Activity lost by cells from 50 cc. of medium in counts per minute	Percentage exchanged
Low concentration (45.5 μgA P/L)	43,980	986	2.2
High concentration (1,137.5 μgA P/L)	465,700	80,716	17.3

REDISTRIBUTION OF INTRACELLULAR PHOSPHORUS

Phosphorus exchange is difficult to detect in a culture with a growing population; however, in the filter-washing experiments, exchange was shown. It was further found that the quantity of phosphorus exchanged depended on the amount of phosphorus in the inorganic fraction in the cells. Whether or not the small amount of phosphorus remaining in the medium at the end of the uptake experiment was due to exchange is not known. For this trace of phosphorus to be the result of exchange would require that some phosphorus always remain in an inorganic state in the cells.

To prepare cells with the inorganic fraction reduced to a minimum necessitates growing them in the light in medium containing no phosphorus. This was the method used to prepare phosphate-deficient cells in the previous experiment. Under these conditions the cells reduce the intracellular phosphorus to a point where further cell division is impossible. Theoretically, under these conditions the inorganic fraction has been reduced to as small an amount as possible.

The rearrangement of intracellular phosphorus was traced in *Nitzschia* cells by following the movement of radioactive phosphorus. To medium containing 14.7 × 10^7 cells per liter were added 8.75 microcuries of radioactive phosphorus. The same amount of radioactive phosphorus was added again the following day. On the second day the cells were centrifuged from this active medium and resuspended in medium with less than 0.5 μgAP/L of nonactive phosphorus. This medium with cells containing radioactive phosphorus was divided into two cultures. One culture was kept in the light while the other was placed in the dark. Ketchum (1939 b) has shown that nondeficient cells similar to these will not absorb phosphorus from the medium in the dark, but it was not shown whether changes occur in the distribution of intracellular phosphorus.

The distribution of intracellular radioactive phosphorus between the organic and inorganic fractions was determined at the time the cells were suspended in the new medium and again on the sixth, tenth, and fourteenth days. The cells were fractionated with trichloracetic acid, as described in Materials and Methods, and radioactivity counts were made on each fraction. The results of this experiment are shown in table 4. The cells kept in the light continued to combine inorganic phosphorus into the organic fraction for most of the 14 days. At the end of this time, 14.7 percent of the radioactive phosphorus still remained in the inorganic state. Under the conditions of this experiment, cell division had stopped by the sixth day. It can be seen in table 4 that little inorganic phosphorus was converted into the organic fraction after cell division stopped. The ceasing of cell division could not have been due to the lack of some other nutrient since the medium contained sufficient amounts of all nutrients except phosphorus. The occurrence of phosphorus in the inorganic fraction at the end of 14 days may indicate that some inorganic phosphorus is always present in *Nitzschia* cells and that division is stopped not by a complete disappearance of inorganic phosphorus but rather by the reduction of the inorganic phosphorus below a threshold amount. From these findings it appears that the trace of phosphorus remaining in the medium in the phosphorus-uptake experiment can be attributed to exchange between the cells and medium.

TABLE 4.—*Distribution of intracellular radioactive phosphorus in* Nitzschia *cells suspended in medium containing only a trace of nonradioactive phosphorus*

[The cells had previously grown for 2 days in medium with phosphorus of high specific activity]

Length of time in new medium	Culture placed in light		Culture placed in dark	
	Inorganic fraction	Organic fraction	Inorganic fraction	Organic fraction
	Percent	*Percent*	*Percent*	*Percent*
0 days	[1] 63.0	[1] 37.0	[1] 63.0	[1] 37.0
6 days	19.1	80.9	59.2	40.8
10 days	20.7	79.3	66.0	34.0
14 days	14.7	85.3	53.4	46.6

[1] Determined before dividing cells into two cultures.

There was not as much change in the distribution of phosphorus between the inorganic and organic fractions in the cells kept in the dark as in those grown in the light, yet there was a slight decrease in the inorganic fraction except on the tenth day (table 4). This one determination was undoubtedly in error. From the data for cells grown in the dark, it can now be surmised that a slight metabolic activity is going on which requires the redistribution of intracellular phosphorus.

EXCHANGE BY CELLS SUSPENDED IN CULTURE MEDIUM

Exchange in the light

The difficulty of detecting phosphorus exchange between cells and medium when phosphorus is being absorbed rapidly by the cells has been shown previously. However, if large amounts of radioactive phosphorus can be incorporated into the cells in a short enough period of time to prevent much from being combined into organic compounds, there is greater possibility of detecting exchange by measuring the loss of radioactive phosphorus from the cells. It must also be considered that, since each cell takes part in the exchange process, the total amount of radioactive phosphorus exchanged from the cells will depend upon the number of cells used. If a large number of dividing cells are used, a high concentration of phosphorus in the medium is needed. Further, if the concentration of phosphorus in the medium is not sufficient, the radioactive phosphorus exchanged from the cells to the medium will be reabsorbed in too large an amount to permit a detection of exchange.

A culture of *Nitzschia* with 22.7 × 10^7 cells per liter in medium containing 2 microcuries of radioactive phosphorus per 100 cc. and a phosphorus concentration of less than 0.5 µgA/L was prepared. It was found that cells could absorb this amount of phosphorus within 20 hours and yet retain most of the radioactive phosphorus in the inorganic state. The cells were then centrifuged from this medium and resuspended in new medium containing 2,000 µgAP/L of nonradioactive phosphorus. It has been found that very little reduction in the division rate of *Nitzschia* occurred in this concentration. This new culture was placed in the culture cabinet in the light. Aliquot samples of 25 cc. each were removed periodically, and the cells were filtered from the medium so that radioactive measurement could be made on the culture medium. The sampling was continued over a period of 14 days (table 5).

TABLE 5.—*Loss of radioactive phosphorus to medium by photosynthesizing and dividing cells*

[The cells of 25 cc. of medium contained 9,728 counts per minute]

Length of time	Activity in 25 cc. of medium in counts per minute	Length of time	Activity in 25 cc. of medium in counts per minute
0.5 hour	169	50.0 hours	219
1.0 hour	202	80.0 hours	368
4.0 hours	212	150.0 hours	493
7.0 hours	202	198.0 hours	601
14.0 hours	234	246.0 hours	621
25.0 hours	231	342.0 hours	678

Phosphorus exchange did occur, since radioactive phosphorus from the cells appeared in the medium. The increase in radioactivity in the medium was rapid at first and then decreased with time. Thus, it has been shown that cells, while absorbing and converting phosphorus into organic compounds, do exchange phosphorus with the medium. The radioactive phosphorus in the medium continued to increase until 6.97 percent of the total radioactive phosphorus contained in the cells had been exchanged to the medium at the end of 14 days.

Exchange in the dark

Ketchum (1939 b) has demonstrated that phosphate-deficient cells placed in the dark will continue to absorb phosphate only for about 10 hours. He also showed that the amount of phosphate absorbed in the dark by phosphorus-deficient cells depends on the length of time the cells have been grown in the light in medium containing no phosphate. From these findings it can be concluded that any uptake of radioactive phosphorus by cells can be attributed to exchange if radioactive phosphorus is added to the medium after the phosphate deficiency of the cells has been replaced.

Exchange determined with radioactive phosphorus in the medium.—A culture of 45 × 10^7 cells per liter was prepared in medium containing 46 µgAP/L. The cells used to prepare this culture came from a medium containing phosphorus. However, to be sure that the cells had no phosphate debt, they were placed in the dark for 16 hours in medium containing phosphorus. The cells were then centrifuged from this medium and resuspended in identical medium to which 0.45 microcuries of radioactive phosphorus per 100 cc. had been added. The culture was again placed in the dark and only removed periodically for sampling. The cells were filtered from aliquot samples of medium, and counts were made for radioactivity in the cells. Inorganic-phosphorus determinations were also made on the medium from each sample. Exchange does occur, as shown by radioactive phosphorus appearing in the cells (table 6). Although the uptake of radioactive phosphorus is small, it is believed to be representative of the amount exchanged, since corrections for contamination were made. This was accomplished by filtering the medium containing the same quantity of radioactive phosphorus and determining the activity retained on the filter, in the $BaSO_4$ precipitate, and on the filter paper. The counts appearing in table 6 were then obtained by subtracting the counts due to contamination from the observed cell-activity count. Of the total radioactive phosphorus in the medium, about 2.5 percent was exchanged with the cells. There was no detectable change in the inorganic-phosphorus concentration of the medium.

TABLE 6.—*Uptake of radioactive phosphorus by cells from medium when kept in the dark*

[The medium contained 9,887 counts per minute]

Length of time	Activity in cells from 25 cc. of medium in counts per minute	Inorganic phosphorus of medium in µgAP/L
0.5 hour	154	46
2.5 hours	178	46
5.0 hours	224	46
22.5 hours	148	46
26.0 hours	245	46

Exchange determined with radioactive phosphorus in the cells.—Since a tendency for the cells to clump in the previous experiment possibly caused one determination to be low, this experiment was devised with the active phosphorus inside the cells so that determination could be made on the medium. To test for the loss of radioactive phosphorus from the cells through exchange, a culture of 40 × 10^7 cells per liter was prepared with 1 microcurie of radioactive phosphorus per 100 cc. of medium and less than 0.5µgAP/L. After 16 hours the culture was centrifuged, and the cells containing radioactive phosphorus were suspended in new medium containing 56 µgAP/L of nonradioactive phosphorus. This culture was placed in the dark and samples were removed periodically. There was a loss by exchange of radioactive phosphorus from the cells to the medium (table 7). Of the total radioactive phosphorus in the cells, 3.26 percent was exchanged with the medium.

TABLE 7.—*Loss of radioactive phosphorus to medium by cells kept in the dark*

[The cells from 25 cc. of medium contained 22,570 counts per minute]

Length of time	Activity in 25 cc. of medium in counts per minute	Length of time	Activity in 25 cc. of medium in counts per minute
0.5 hour	87	12.0 hours	519
1.2 hours	155	24.5 hours	615
2.0 hours	175	28.0 hours	746
3.5 hours	210	34.0 hours	735
5.5 hours	325		

DISCUSSION

Some investigators have found it necessary to wash the cells before using them for chemical analysis. According to Gest and Kamen (1948), the washing liquid is usually distilled water, 0.85 percent saline, or less frequently, fresh culture medium. Washing with a saline solution is less drastic than with distilled water. Even so, many organisms have been found to lose phosphorus when washed with saline solutions. A young culture of *Bacterium coli*, after two washings with a saline solution, showed a rapid release of inorganic phosphorus in the absence of glucose (Macfarlane 1939). Also an appreciable quantity of the original phosphorus of *Trypanosoma equiperdum* is lost when the organisms are washed with saline solution (Moraczewski and Kelsey 1948). It must be pointed out, however, that this type of experiment does not demonstrate exchange. For phosphorus exchange to occur, there must be a movement of equal numbers of phosphorus atoms both into and out of the cells. This naturally precludes interpreting the above observations as being exchange, since neither distilled water nor saline solutions ordinarily contain phosphorus.

Fresh-water algae grown in high-phosphate media have been shown to store an appreciable quantity of soluble phosphate which is readily lost when the cells are washed with medium (Gest and Kamen 1948). Also marine species of algae exchange phosphate to a nutrient medium when filter-washed, as has been shown by Goldberg, et al. (1951) and in the experiments reported in this paper. Even with the use of radioactive phosphorus which makes possible an altering of the isotopic distribution of phosphorus in either the medium or the cells, exchange is still difficult to demonstrate, especially in rapidly dividing unicellular forms. This is because the amount of phosphorus absorbed by the cells is many times greater than that leaving the cells through exchange.

Goldberg, et al. (1951) stated that as much as 50 percent of the phosphorus is removed from the marine diatom *Asterionella* when it is washed with sea water; but the factors controlling this removal of radioactive phosphorus from the cells were not discussed. In the filter-washing experiments conducted in this investigation, *Nitzschia* cells were always washed with a culture medium containing the same concentration of nonradioactive phosphorus as that of the medium in which the cells had previously grown. The amount of phosphorus exchanged with the medium when filter-washed in this manner was found to vary with the physiological condition of the cells. Phosphate-deficient cells grown for the same period of time in medium containing radioactive phosphorus not only absorbed more phosphorus than nondeficient cells, but also exchanged a smaller percentage of that absorbed when filter-washed. Regardless of the condition of the cells, the amount exchanged varied with the phosphorus concentration of the medium in which the cells were grown. Those grown in a high phosphorus concentration not only absorbed more phosphorus but also exchanged more phosphorus with the washing medium.

The percent of radioactive phosphorus exchanged by the cells also depends on the length of time the cells have been grown in radioactive phosphorus. In the filter-washing experiments, nondeficient cells grown for 7 days in the presence of radioactive phosphorus exchanged a smaller percent of radioactive phosphorus than the same type of cell grown in a similar medium for 20 hours. This was the result of more radioactive phosphorus being converted into organic or nonexchangeable compounds in cells grown for the longer period of time. Thus, a smaller percent of the radioactive phosphorus in the cells was exchanged with the medium even though the total phosphorus exchanged in both instances possibly was the same.

In cultures of rapidly dividing unicellular forms, the organic matter increases at a fast rate, quickly removing both radioactive and nonradioactive phosphorus from the medium and thus complicating the measurement of exchange. It is less difficult to detect exchange by measuring the movement of radioactive phosphorus from the cells to a medium continually renewed and containing only nonradioactive phosphorus, provided the specific activity of the exchangeable phosphorus of the cell is high. These were the conditions in the filter-washing experiments. Since under most conditions some radioactive phosphorus remains in the inorganic fraction of the cell and the addition of large amounts of phosphorus to the medium causes an increase in the amount of phosphorus exchanged by the cell, exchange of radioactive phosphorus from the cell can also be detected by increasing the phosphorus concentration of the medium instead of continually renewing it. By following this procedure, phosphorus exchange was measured between dividing cells maintained in the light and the culture medium. While exchange is easily demonstrated by filter-washing, the experiments conducted in the light and in the dark may be more representative of normal exchange.

In the exchange experiment in the dark the cells were in equilibrium with phosphorus in the medium before the radioactive phosphorus was added. The actual amount of phosphorus added with the radioactive phosphorus in terms of μgAP/L was insignificant. Since the cells had remained in the culture cabinet long enough for any phosphate deficiency to have been repaid and, therefore, any absorption of phosphorus from the medium to have stopped, the appearance of radioactive phosphorus in the cells indicated that phosphorus exchange had occurred between cells and medium. In some instances it is only possible to measure exchange over short periods of time; however, it should not be concluded that exchange ceases when it is no longer possible to detect it, but rather that both the radioactive and nonradioactive phosphorus of the medium and the cells have reached equilibrium. Thus, neither a further absorption of phosphorus from the medium nor exchange would alter the specific activity, without which exchange cannot be demonstrated.

In the experiments conducted in the light and in the dark the amount of phosphorus exchanged was very small. It may be questioned whether there was not an exchange between the phosphorus of the medium and that adsorbed on the surface of the cells instead of the phosphorus from inside the cells. That some of the phosphorus exchanged in these experiments came from inside the cells is supported by several observations. In relation to the total amounts of phosphorus adsorbed, the amounts exchanged in the filter-washing experiments were too large to have been exchanged only with the phosphorus adsorbed on the cell surface. Also it was possible to measure exchange for as long as 24 hours in some experiments and for a longer period of time in the experiment tested for 14 days. It is possible that exchange between intracellular phosphorus and the medium is complicated by biological or other processes of the cell, resulting in a longer time being required for an equilibrium to be reached than if the phosphorus were exchanged only from the surface.

The amount of phosphorus on the surface of the cell may also be directly related to the manner in which phosphorus enters the cell. Two ways in which phosphorus may enter a cell are discussed by Kamen and Spiegelman (1948). One method is believed to be diffusion through the cell membrane of phosphorus as inorganic orthophosphate to combine with the intracellular orthophosphate. Inorganic orthophosphate is assumed to be the source of phosphorus for the various organic phosphates in the cell. The other method is the entry of phosphorus into the cell through esterification at the cellular interface. Intracellular inorganic orthophosphate would then arise primarily from the breakdown of organic phosphate. From their experimental data with yeast these investigators concluded that the primary mechanism of the entrance of phosphate is by esterification.

Phosphorus probably enters algae by one or a combination of these two methods. The mechanism of entry is of importance in phosphorus-exchange studies only if it requires that phosphorus remain on the surface of the cells for any period of time. If the entry of phosphorus into the cell is by diffusion instead of by esterification, it might be very difficult for much phosphorus to be adsorbed on the cell surface, since there would be a tendency for any phosphorus coming in contact with the cell surface to be taken into the cell. The process of esterification, on the other hand, would probably require that phosphorus remain on the surface of the cell for a longer time. Since a population of unicellular algae presents a large surface area, exchange can take place between any phosphorus adsorbed on the surface of the cells and the medium. As far as I can determine there has not been sufficient consideration of the part adsorption plays in phosphorus exchange in microorganisms. It is impracticable to distinguish the phosphorus exchanged from the cell surface from that exchanged from inside the cells. Thus, exchange demonstrated in these studies should be considered to include phosphorus both from the cell surface and from inside the cell.

The amount of phosphorus in phytoplankton varies with the concentration of phosphorus in the medium and some investigators have considered that the minimum phosphorus which can exist in the cell is "bound" phosphate, presumably organic phosphorus. Several observations were made in this investigation which possibly show that all of the minimum phosphate in the cell does not necessarily exist as an organic fraction. It was observed in the phosphorus-absorption experiment that a trace of phosphorus remained in the medium. For this phosphorus to remain in the medium would require that some phosphorus, which could be exchanged with the medium, still remain in the cells. Since a sufficient amount of all other nutrients were present to allow the complete utilization of all the phosphorus, it appears that some phosphorus was still present in the inorganic fraction of the cells. It is well known that cells placed in culture medium containing no phosphorus will continue to divide until they become phosphorus deficient. These cells then could contain only a minimum amount of phosphorus. Cells containing radioactive phosphorus and placed in medium containing only a trace of phosphorus continued to divide and reduce the inorganic-phosphorus fraction for several days. However, after all division had stopped some radioactive phosphorus remained in the inorganic fraction. Thus it appears that some of the minimum phosphorus of the cell may remain in the inorganic fraction.

Hutchinson and Bowen (1950) added radioactive phosphorus at the surface of Linsley Pond and studied its movement over a 4-week period in summer. It appeared that practically all the radioactive phosphorus entered the phytoplankton immediately and that the rate of regeneration was rapid. This continual release of phosphorus from decomposing organisms, which could be mistaken for exchange, is one of several factors in operation tending to complicate exchange studies under natural conditions. Of course, phosphorus lost in this manner could only remain in the water and subsequently be mistaken for exchange when the concentration of phosphorus in the water was already greater than the demands of the organisms. If a lack of phosphorus limited cell division, any phosphorus returned to the water through either regeneration or exchange would be absorbed immediately and any possibility of its detection would be eliminated. However, with cultures grown in the laboratory it is possible to reduce decomposition of cells to an insignificant point and thus eliminate the effect of regeneration. Also, it is possible to control the phosphorus concentration in the medium so that any radioactive phosphorus exchanged from cells to medium can be measured before being reabsorbed by the cells. Thus it can be concluded that while phosphorus absorption and regeneration can be followed in nature, as shown by Hutchinson and Bowen, the measurement of exchange is limited to the laboratory where conditions can be more closely controlled.

SUMMARY

1. Phosphorus exchange between culture medium and marine planktonic algae was demonstrated.
2. The amount of phosphorus exchanged by *Nitzschia* cells when filter-washed varied with the concentration of phosphorus in the medium in which the cells were grown and with the physiological condition of the cells.
3. The percent of radioactive phosphorus exchanged from cells depends upon the length of time the cells are grown in the presence of radioactive phosphorus. It was found that cells grown over longer periods of time converted more radioactive phosphorus into organic or nonexchangeable compounds.
4. A redistribution of intracellular phosphorus between the inorganic and organic fractions occurred when cells were placed in the light in medium containing only a trace of phosphorus. Cells kept in the dark converted very little intracellular inorganic phosphorus into the organic state.
5. Exchange between photosynthesizing and dividing cells and culture medium was demonstrated by placing cells containing radioactive phosphorus in nonactive medium and measuring the radioactive phosphorus exchanged from the cells to the medium.
6. Exchange between cells and medium was shown while the cells were not photosynthesizing and dividing.

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FOOD OF YELLOWFIN TUNA IN THE CENTRAL PACIFIC

By JOHN W. REINTJES and JOSEPH E. KING

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ABSTRACT

The stomachs of 1,097 yellowfin tuna (*Neothunnus macropterus*) were collected in the central Pacific in 1950 and 1951, and their contents analyzed quantitatively. The tuna were captured by trolling, pole-and-line, and longline, came from different habitats—inshore and offshore, surface and subsurface—and were of different size groups. The results show that the yellowfin accepts a great variety of animal food, from plankton to large fish and squid. Of the total volume of food remains, 47 percent was fish, 26 percent squid, and 25 percent crustaceans. A total of 38 fish families and 11 major invertebrate groups was represented.

Composition of the food varied considerably with size of yellowfin and locale of capture, whether surface or subsurface, near shore or offshore. Comparison of the average volumes of stomach contents indicated that yellowfin from offshore areas contained as much food in their stomachs as those captured just off the reef; and those from subsurface levels as much as those from the surface. Feeding took place during daylight hours.

Yellowfin captured in the zone of high zooplankton abundance near the Equator contained greater amounts of food in their stomachs than those captured at more northerly or southerly latitudes. Since most elements of the pelagic fauna appear to be acceptable as food, distribution and abundance of the yellowfin is probably determined not by the occurrence of any specific food items but rather by the total amount of food organisms present in an area.

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FOOD OF YELLOWFIN TUNA IN THE CENTRAL PACIFIC

By John W. Reintjes and Joseph E. King
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The Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service is authorized [1] and directed to gather information to ensure maximum development and use of the high-seas fishery resources of the territories and island possessions of the United States in the tropical and subtropical Pacific. Since the tunas constitute the group of pelagic fishes having the largest and most immediate economic potential in this region, research has been concentrated on species of this group.

In view of the recognized importance of food as an environmental factor influencing the distribution of fish, a study was initiated to determine what tunas eat, and how the abundance and distribution of food organisms are related to the abundance and distribution of tunas. The first part of the study has been accomplished with a reasonable degree of completeness for the yellowfin tuna, *Neothunnus macropterus* (Temminck and Schlegel), and the results are presented in this report. Further study of the abundance and distribution of tuna is needed.

The yellowfin tuna occurs in all parts of the tropical Pacific. In recent years it has constituted 50 to 60 percent of the catch of the live-bait tuna fishery of the west coasts of the Americas. The longline fishery in the vicinity of the Hawaiian Islands depended on the yellowfin for more than 50 percent of its catch in the years 1945–48 (June 1950). The species also comprises about 50 percent of the catch of the Japanese longline fishery in the tropical western Pacific. It is taken by native peoples and sport fishermen throughout its range.

The literature contains many references to the food of yellowfin. Most of these, however, are based on casual observations made on small samples of fish, or refer to material regurgitated by the fish when it was landed. Observations by the following authors are worthy of mention.

Kishinouye (1917, 1923), reporting on the food of yellowfin captured by longline fishing in the Bonin Islands, stated that they feed on flyingfish, "coffer fish," "some deep-sea fish," "calamaries," pteropods, heteropods, hyperid amphipods, larval and immature *Squilla*, and the megalops of crabs. Okuma, Imaizumi, and Maki (1935) noted that large amounts of small skipjack, shrimp, small crabs, carangids, and balistids were found in yellowfin stomachs collected in Indo-Pacific waters. Nakamura (1936, 1943), from an examination of the stomach contents of yellowfin captured by longline gear in the Celebes Sea, reported clupeoid, scombroid, and plectognath fishes among the most common food items, followed by squid and palinurids, squillids, syllarids, and *Leander* among the crustaceans.

Walford (1937) reported that flyingfish, sauries, sardines, squid, and larval and adult planktonic crustaceans were found in the stomachs of yellowfin captured by surface fishing in the coastal waters of the eastern Pacific. Marukawa (1939) examined 12 longline-caught yellowfin from equatorial waters south of the Palaus, and briefly summarized the results in a checklist which includes fishes, squid, and crustaceans. Kanamura and Yazaki (1940a, 1940b) found squid, triggerfish, balloonfish, and shrimp in the stomachs of longline-caught yellowfin from the East Philippine Sea and the South China Sea. Ban (1941) reported the occurrence of planktonic animals, paper nautilus, trunkfish, juvenile carangids, mackerel, sphyraenids, and mature skipjack among the stomach contents of yellowfin. Ikebe (1942) stated that yellowfin captured in waters southwest of New Guinea were feeding mostly on squid. Suyehiro (1942) reported briefly on the stomach contents of a "sample" taken during one day's fishing off southern Japan. In addition to his own observation he reported that leatherfish, cuttlefish, and shrimp were found in the stomachs of yellowfin taken near Timor Island.

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[1] Public Law 329, 80th Congress.

Tinker (1944), Chapman (1946), and Hildebrand (1946) briefly referred to the food of the yellowfin tuna as consisting of small shore and pelagic fishes, squid, and planktonic crustaceans. Herald (1949) found a 42-millimeter seahorse, juvenile surgeonfish, triggerfish, and other common forms in the stomach of a yellowfin taken near the Hawaiian Islands. Fitch (1950) found large numbers of postlarvae of the pointed-tailed ocean sunfish (*Masturus lanceolatus*) in yellowfin from Hawaiian waters.

All of these investigators listed the kinds and, in a few cases, the numbers of organisms that were found in the stomachs of yellowfin tuna, but they gave no quantitative analysis of the relative importance of the various food elements or their relation to locality, habitat, or body size of the tuna concerned. Welsh (1949), on the other hand, has made a quantitative study of the food of the yellowfin, but only 20 relatively small specimens, all captured within ½ mile or less of Oahu, Hawaiian Islands, were examined. Ronquillo (1950) examined the stomachs of 144 yellowfin from the waters of the southern Philippines and made a preliminary report and checklist of organisms found and their frequency of occurrence.

The authors are grateful to fellow staff members, ships' officers and crews of the *Hugh M. Smith*, *John R. Manning*, and the *Henry O'Malley*, for their assistance in handling these large fish at sea and in removing and preserving the stomach material.

SOURCE OF MATERIALS

Material collected in 1950 and 1951, during 12 cruises of Fish and Wildlife Service vessels [2] in waters surrounding the Line and Phoenix Islands, was available for this investigation (table 1). Of the 5,164 yellowfin captured on these cruises, the stomachs from 1,097 were preserved for subsequent analysis. Of the 1,097 fish sampled, 786 were taken at the surface by trolling or by live-bait pole-and-line fishing, and 311 were caught at depths of 100 to 500 feet with longline gear.[3] A total of 775 of the surface-caught fish and 70 of those taken on longlines were captured within 10 miles of land (table 2). The remaining 11 surface-caught fish and 241 subsurface-caught fish were taken in waters 10 miles or more from land.

The sampled yellowfin ranged widely in size, from approximately 500 to 1,700 millimeters (5 to 200 pounds). The length distribution of these fish is given in figure 1. For purposes of comparison the fish were classified in three size categories: (1) small, less than 1,000 mm. fork length, or approximately 43 lb.; (2) medium, 1,000 to 1,299 mm.

TABLE 1.—*Distribution of the yellowfin tuna taken and stomachs collected in the central Pacific, by time of year, cruise, locality, and fishing method, 1950 and 1951*

Time of year	Vessel	Cruise	Locality	Fishing method	Number of yellowfin captured	Number of stomachs examined	Percent of catch sampled
1950							
February	Hugh M. Smith	2	Phoenix Islands	Trolling	10	9	90. 0
				Pole-and-line	4	4	100. 0
April-June	John R. Manning	2	Line Islands	Trolling	882	105	11. 9
July	Hugh M. Smith	5	Phoenix Islands	Longline	53	52	98. 1
				Trolling	2	2	100. 0
July-August	Henry O'Malley	4	Phoenix Islands	Trolling	24	7	20. 8
				Pole-and-line	271	24	15. 4
August	Henry O'Malley	4	Line Islands	Trolling	4	2	50. 0
				Pole-and line	8	5	62. 5
	John R. Manning	3	Phoenix Islands	Trolling	64	41	64. 1
September	John R. Manning	3	Line Islands	do	109	21	19. 3
November	Hugh M. Smith	7	do	Trolling	5	4	80. 0
				Longline	132	106	80. 3
	John R. Manning	4	do	Trolling	98	96	98. 0
1951							
January-February	Hugh M. Smith	8	do	do	25	23	92. 0
	John R. Manning	5	Phoenix Islands	do	27	23	85. 2
February	John R. Manning	5	Line Islands	do	43	27	62. 8
April-May	do	6	do	do	110	100	90. 9
June	Hugh M. Smith	9	Line Islands	Trolling	29	19	65. 5
				Pole-and-line	2, 628	209	8. 0
			Phoenix Islands	Trolling	2	2	100. 0
				Pole-and-line	177	63	35. 6
August-September	do	11	Line Islands	Longline	457	153	33. 5
Percent of total sampled							21. 2

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[2] The *Hugh M. Smith*, *John R. Manning*, and *Henry O'Malley*.

[3] The live-bait method of tuna fishing has been described by Godsil (1938), the longline method by Shapiro (1950) and June (1950), and surface trolling by Bates (1950).

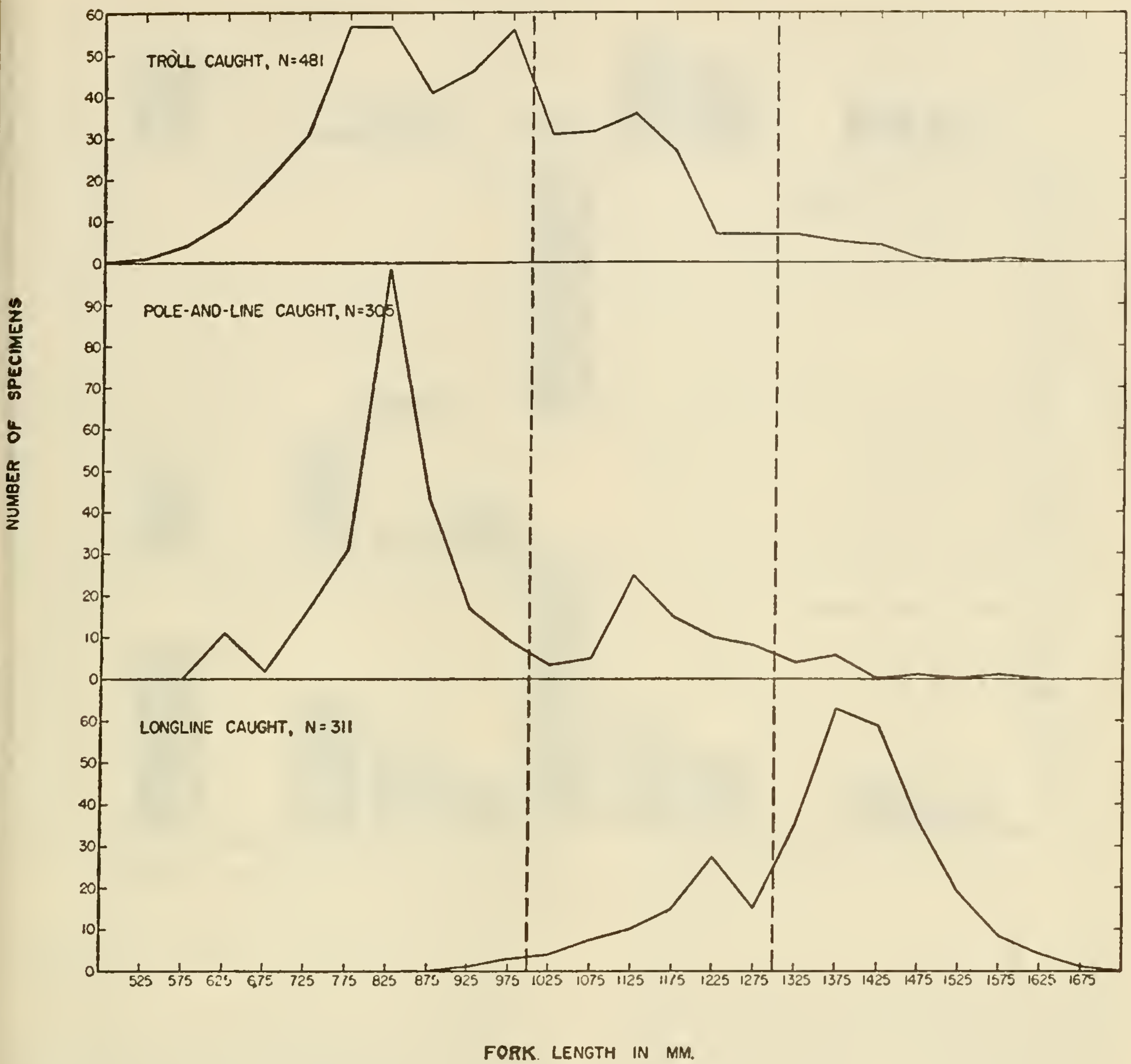

FIGURE 1.—Length distribution of sampled yellowfin according to method of capture. N=number of fish.

TABLE 2.—*Distribution of 1,097 yellowfin-tuna samples, by distance of capture from land and fishing method*

Distance from land	Trolling	Pole-and-line	Longline
0 to 9 miles	470	305	70
10 to 24 miles	5		27
25 to 49 miles	1		12
50 to 99 miles			27
100 to 199 miles	1		37
200 to 499 miles	4		124
500 miles and more			14
Total	481	305	311

fork length; and (3) large, 1,300 mm. and over, fork length, or about 94 lb. or more. These size classes were established to provide an intermediate size range which would include comparable numbers of fish captured by all three fishing methods.

The collections were made chiefly in three general localities: the Phoenix Islands, the Line Islands, and the open ocean to the east and west of the Line Island group. Although the sampling was fairly well distributed over the 2-year period,

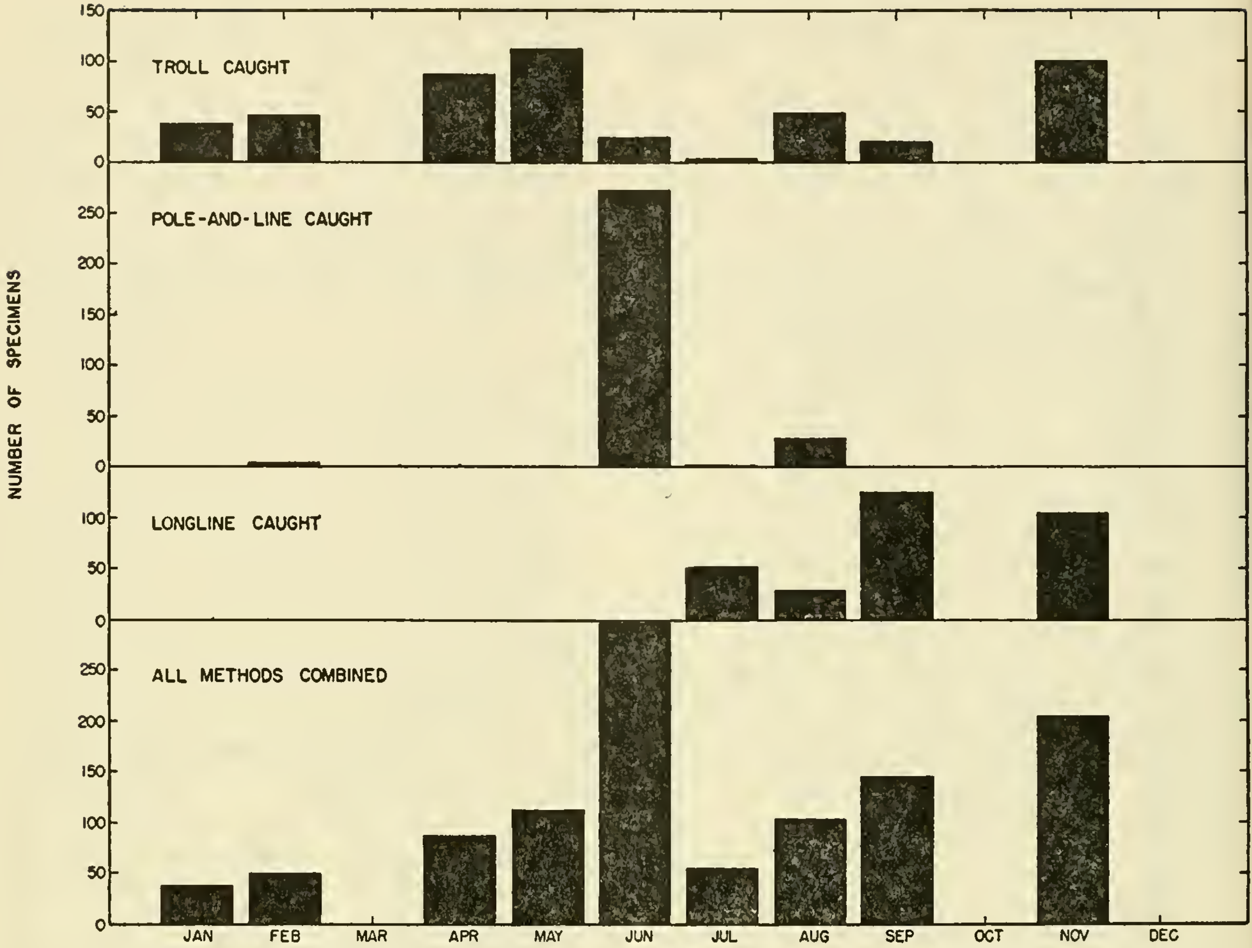

FIGURE 2.—Distribution of yellowfin stomach collections, by month and by method of capture, February 1950 to September 1951.

it was not distributed over the months of the year for each fishing method as well as desired. Figure 2 indicates, for each method of capture and for all methods combined, the number of stomachs obtained during each month, the years 1950 and 1951 combined.

METHODS

COLLECTION OF MATERIALS

In the field, the stomach was removed as soon as possible after the fish was captured, placed with any regurgitated material in an unbleached muslin bag, and preserved in 10-percent formalin. A label bearing the date, the locality, the method, depth, and time of capture, the species, fork length, bait used, name of observer, and vessel, was placed with each stomach.

The stomach was removed by one of the following methods:

(1) The abdominal cavity was opened by a longitudinal midventral incision, the small intestine severed posterior to the pyloric valve, and the stomach freed by cutting through the muscular esophagus.

(2) The gill membrane was slit along the line of attachment with the cleithrum, posterior to the fourth gill arch, the viscera pulled out, and the stomach removed by cutting through the small intestine and esophagus.

IDENTIFICATION OF STOMACH CONTENTS

In the laboratory, the stomachs were leached in fresh water for a period of 12 to 24 hours to remove excess formalin. All of the contents were carefully removed and separated into groups.

Each organism was identified as completely as was practicable and the number of each species or group of organisms was recorded. Each subdivision or kind of food was then measured volumetrically by the displacement of water in a graduated cylinder of appropriate size. Bait used to capture the yellowfin was not considered in this analysis.

The methods used to identify food organisms and organic remains varied to a great extent, and depended on the group of animals under consideration. The arthropods were identified to taxonomic order from general exoskeletal characteristics. Although Euphausiacea, Mysidacea, and Decapoda were difficult to separate, the scarcity of the first two orders made the problem of secondary importance. Amphipoda, Isopoda, Stomatopoda, and most Decapoda were easy to distinguish to taxonomic order even with partial remains. Some members of the amphipod families of Calliopiidae, Hyperiidae, Oxycephalidae, and Gammaridae found in this region were recognized by certain cephalic characteristics and body shape. The species of Stomatopoda, which even when badly damaged were readily distinguished by certain exoskeletal features, have been described by Brooks (1886), Kemp (1913), Edmondson (1921), Bigelow (1931), and Townsley (1950), who reported on Pacific forms and constructed keys for their separation. Such decapod crustaceans as the postlarval Palinuridae and Nephropsidae were readily identified because each possesses unique familial traits. Identification of the latter family was aided by the work of Holthius (1946).

The shelled molluscs found in the stomachs of tuna were readily identified as heteropods, pteropods, and nautiloid cephalopods from distinguishable shell remains. The cephalopods were separable to squid and octopods on the basis of general body shape, number of arms, presence or absence of a gladius (pen), and modification of suckers into hooks. The presence of tentacles (fifth pair of arms) was used as a distinguishing trait in all squid except in the aberrant family of eight-armed squid, Octopodoteuthidae, where the modification of suckers into hooks indicated a decapod mollusc. Berry (1914) used the perforation of the eyelid, arrangement of the suckers, and the hectocotylus (modification of one tentacle into an accessory sex character in the male) to distinguish genera and species of cephalopods; however, all of these structures are susceptible to the destructive action of the digestive juices so that in most instances organisms were identifiable only as squid or octopods.

Pelagic tunicates were seldom identifiable to family because the soft body readily disintegrated into gelatinous fragments in the tuna stomach. These remains retained certain characteristics, however, that distinguished them from the coelenterates and pelagic molluscs with similar gelatinous structure.

The teleost fishes were readily recognized by their skeletal remains. Further identification, even to taxonomic order, was dependent on certain traits, many of which were readily lost. Engulfment often separated the head from the body, mutilated the fins, skin, and lateral line, and removed scales, making identification difficult. Fishes with bony protuberances, carapace-like integument, and other distinguishable hard parts were the most easily identified. Familial identification was often dependent upon singular characteristics, such as bony scutes in the Carangidae and teeth and mandibles in the Tetrodontidae, Diodontidae, Alepisauridae, Aulostomidae, Belonidae, and Hemirhamphidae. In more generalized groups possessing neither unique nor resistant parts, identification could not be easily made. Juvenile fishes often lack traits characteristic of the adults; for these, identification to the family frequently was impossible. It is estimated that 80 percent of the fish specimens could be identified to family.

The most useful references for the identification of fishes were Fowler (1928, 1931, 1934, 1949), Jordan and Evermann (1905), Gilbert (1905), Weber and De Beaufort (1913–1936), De Beaufort (1940), Schultz (1943), Brock (1950), and De Beaufort and Chapman (1951). Berg's (1947) modification of Regan's system of classification was used for the forage fishes. A reference collection of invertebrates and fishes maintained at our laboratory in Honolulu was used intensively during the study.

EVALUATING FOOD COMPONENTS

Three general systems of analysis and methods of expressing results have evolved from the many investigations of the stomach contents of fish, birds, mammals, and other animals. These systems might be termed the "numerical," the "frequency of occurrence," and the "volumetric." Each has its shortcomings, some of which are inherent in the nature of the problem, and at best it can afford only a rough indication of the food habits of the animal.

The numerical system is based solely on a count of organisms present, with each food element evaluated as a percent of the total number of all elements. This method tends to place undue emphasis on food organisms with very resistant parts. In summing up the food of a number of individuals, instead of getting a cross section of the most recently obtained food, a record is obtained of the more durable elements of past and recent food and a false idea of the food may result. Furthermore, the numerical system does not take into account the size of objects, and hence conveys little of the relative importance of the separate components in terms of bulk since the numerical majority may form but a small proportion of the food. Foods that have become finely broken up can be only roughly estimated by number. Also, the time required for the investigator to make an accurate count, as for example, of the thousands of crab larvae in the stomach of a tuna which has gorged itself on this food, may be prohibitive, necessitating the use of an estimation based on a subsample.

In frequency-of-occurrence analysis, each food element is expressed as a percentage computed by dividing the number of stomachs containing the food, regardless of amount, by the total number of stomachs examined. This provides a rough but useful index to the overall availability, and perhaps the palatability, of the food element.

The volumetric system is based on percentage by bulk. Its use reduces the overevaluation of food organisms with more durable parts to a minimum. A large series of stomachs yields reliable information on recent food, with old food represented by traces. The size of individual items is taken into account only by this system. As with the other two methods of analysis, some soft-bodied organisms may leave no appreciable trace in the stomach and thus may be underrated in importance. Other errors may result from different digestion rates. Hess and Rainwater (1939), for example, demonstrated that of the different kinds of immature insects fed to brook trout, small soft-bodied forms were digested more rapidly than large thick-skinned types. Karpevich (1941) found that Gammaridae were digested more rapidly by three marine fishes than were larger crustaceans and small fish. Despite its defects, we believe this system to be the best of the three, if conclusions are to be based on but one method of analysis.

The volumetric system can be used in several ways to evaluate the amount of each kind of food present. Martin, Gensch, and Brown (1946), for example, describe the following two ways:

Aggregate-total-volume method: The percentage for each kind of food is obtained by dividing the total volume of all food of each kind by the total volume of the stomach contents of all the fish. The variation in the total volume of food from each stomach influences the final result in direct proportion to that volume.

Average-percentage method: Percentage equivalents are calculated for each food item with each stomach evaluated 100 percent regardless of the volume of its contents. Variation in the total volume of food present, therefore, does not influence the results. Stomachs containing very little food exert the same influence on results as do well-filled stomachs.

The aggregate-total-volume method has the definite merit of reflecting truly the volumetric importance of a particular food organism regardless of whether much or little of other foods is present.

Various combinations of the three basic systems of analysis have been devised to present a more complete picture of the food habits of the animal being studied. Tester (1932) combined the volumetric and the frequency-of-occurrence methods for a graphic representation of the food of the smallmouth black bass, *Micropterus dolomieu*. The relative importance of each kind of food was demonstrated graphically by a rectangle in which the percentage volume of a kind of food was the horizontal line and the percentage frequency-of-occurrence was the vertical. The vertical scale was arbitrarily fixed at 40 percent of the horizontal to give the volume of food more weight. In a different method devised by Welsh (1949), each kind of food was evaluated by a percentage rating which was "an average of the percent of the total bulk of the individual food used (indicating food value), the total number of individual food-animals used (indicating abundance), and the total number of stomachs in which the individual food were found indicating availability." Although this final averaged-percentage figure appears to be a combination of dissimilar terms, it perhaps serves as a simplified and useful index.

Throughout this investigation, as complete records as possible were kept on the contents of each stomach so that all necessary information would be available for whatever method or methods of analysis were finally decided on. In reviewing the results of the study, it appeared that all three of the basic methods were necessary for proper evaluation of the food of the yellowfin. Therefore, in table 3, which gives the detailed results of the study, there is shown for each food element the total number of such organisms in all stomachs, the number of stomachs in which it occurred, the percent frequency of occurrence, the aggregate total volume of such organisms in all stomachs, and the percent aggregate total volume.

Regardless of the method of analysis used, there are many uncontrollable variables inherent in food studies which detract from the precision of the results. One may safely conclude, however, that those food items that rank large in number, large in volume, and high in frequency of occurrence are important foods—at the time and in the area sampled.

TABLE 3.—*Checklist of food organisms found in the stomachs of 1,097 yellowfin tuna captured in the central Pacific, 1950 and 1951*

Food organisms	Number of organisms	Stomachs in which occurred		Aggregate total volume	
		Number	Percent	Cc.	Percent [1]
ARTHROPODA					
Crustacea	[85, 140]	[734]	[66. 9]	[12, 991. 1]	[24. 8]
Mysidacea					
Oplophoridae:					
Oplophorus foliaceus	20	1	.1	105. 0	.2
Unidentified mysids	4	2	.2	.6	--------
Amphipoda					
Hyperiidae	251	80	7. 3	78. 0	.2
Oxycephalidae	11	4	.4	2. 3	--------
Oammaridae	1	1	.1	.2	--------
Calliopiidae	2	1	.1	.5	--------
Unidentified amphipods	202	50	4. 6	58. 3	.1
Isopoda	7	3	.3	1. 2	--------
Stomatopoda					
Squillidae:					
Squilla sp. alima	46	7	.6	10. 5	--------
Pseudosquilla ciliata monodactylus stage	3, 574	290	26. 4	1, 186. 5	2. 3
Pseudosquilla oculata erichthus	631	112	10. 2	215. 3	.4
Lysiasquilla sp. erichthus	315	114	10. 4	152. 4	.3
Lysiosquilla n. sp. erichthus and postlarvae	81	34	3. 1	62. 3	.1
Gonodactylus guereni postlarvae	902	148	13. 5	233. 6	.4
Crustacea—Continued					
Stomatopoda—Continued					
Squillidae—Continued					
Odontodactylus hanseni postlarvae	1, 046	142	12. 9	446. 6	0. 8
Unidentified stomatopods	164	61	5. 3	105. 5	.2
Euphausiacea					
Euphausiidae:					
Euphausia sp	35	5	.5	6. 4	--------
Unidentified euphausiids	6	2	.2	2. 0	--------
Decapoda					
Penaeidae:					
Metapenaeus sp	38	4	.4	70. 0	.1
Unidentified shrimp	999	81	7. 4	288. 8	.6
Nephropsidae:					
Enoplometopus sp. postlarvae	905	95	8. 7	295. 0	.6
Palinuridae:					
Panulirus sp.					
phyllosoma (larvae)	7	5	.5	2. 8	--------
puerulus (postlarvae)	18	12	1. 1	16. 0	--------
Unidentified crab larvae					
zoeae	2	2	.2	1. 0	--------
megalops	75, 875	529	48. 2	9, 363 0	17. 9
Paguridae	1	1	.1	.3	--------
Unidentified crustaceans	--------	39	3. 6	287. 0	.5
MOLLUSCA					
Pteropoda					
Cavolinidae:					
Carolinia sp	10	1	.1	6. 0	--------
Unidentified pteropods	1	1	.1	1. 0	--------
Pectinibranchiata (Heteropoda)					
Atlantidae	4	2	.2	1. 0	--------
Unidentified heteropods	99	51	4. 6	169. 2	.3
Decapoda (squid)	[3, 642]	[608]	[55. 4]	[13, 722. 2]	[26. 2]
Onychoteuthidae:					
Onychoteuthis banksi	17	3	.3	66. 0	.1
Ommastrephidae:					
Symplectoteuthis oualaniensis	43	7	.6	309. 0	.6
Octonodoteuthidae	1	1	.1	700. 0	1. 3
Unidentified squid	3, 581	603	55. 0	12, 647. 2	24. 2
Octopoda					
Argonautidae:					
Argonauta hians	3	3	.3	12. 5	--------
Unidentified argonauts	184	41	3. 7	456. 5	.9
Bolitaenidae:					
Eledonella sp	2	2	.2	45. 0	.1
Unidentified octopods	80	26	2. 4	176. 0	.3
CHORDATA					
Tunicata	[240]	[69]	[0. 3]	[300. 0]	[.6]
Salpidae:					
Pyrosoma sp	27	8	.7	76. 0	.1
Unidentified salps	128	43	3. 9	137. 2	.3
Unidentified tunicates	85	16	1. 5	86. 8	.2
Vertebrata (Pisces)	[5, 333]	[772]	[70. 4]	[24, 456. 6]	[46. 7]
Sternoptychidae (hatchetfishes):					
Sternoptyx diaphana	2	1	.1	1. 0	--------
Synodidae (lizardfishes)	2	2	.2	3. 0	--------
Sudidae	3	1	.1	20. 0	--------
Alepisauridae (lancetfishes)	5	4	.4	32. 0	--------
Leptocephalus (larvae)	12	5	.5	7. 2	--------
Myctophidae (lanternfishes)	35	17	1. 5	79. 0	.2
Belonidae (needlefishes)	3	2	.2	52. 0	.1
Hemirhamphidae (halfbeaks)	1	1	.1	30. 0	--------
Exocoetidae (flyingfishes)	23	21	1. 9	1, 740. 0	3. 3
Macruridae (grenadiers)	1	1	.1	2. 0	--------
Aulostomidae (trumpetfishes):					
Aulostomus chinensis	4	3	.3	7. 0	--------
Syngnathidae (pipefishes and seahorses):					
Hippocampus kudo	1	1	.1	1. 0	--------
Unidentified pipefishes	4	2	.2	1. 5	--------
Lophotidae (oarfishes):					
Lophotes capellei	2	1	.1	15. 0	--------
Holocentridae (squirrelfishes)	2	1	.1	6. 0	--------

[1] Given only when 0.1 percent or greater.

TABLE 3.—*Checklist of food organisms found in the stomachs of 1,097 yellowfin tuna captured in the central Pacific, 1950 and 1951*—Continued

Food organisms	Number of organisms	Stomachs in which occurred		Aggregate total volume	
		Number	Percent	Cc.	Percent [1]
Vertebrata (Pisces)—Con.					
Sphyraenidae (barracudas)	1	1	0.1	5.0	--------
Polynemidae (threadfins)	1	1	.1	2.0	--------
Priacanthidae (big-eyes)	6	5	.5	9.0	--------
Carangidae (jacks):					
Decapterus sp	46	24	2.2	4,395.0	8.4
Naucrates ductor	3	1	.1	960.0	1.8
Unidentified jacks	4	4	.4	445.0	.9
Bramidae (pomfrets):					
Taractes sp	28	16	1.5	194.5	.4
Collybus drachme	449	150	13.8	1,756.6	3.4
Unidentified pomfrets	101	21	1.9	171.0	.3
Coryphaenidae (dolphins)	1	1	.1	205.0	.4
Lutianidae (snappers)	48	15	1.4	46.0	.1
Chaetodontidae (butterflyfishes)	24	13	1.2	50.5	.1
Pomacentridae (demoiselles)	14	8	.7	8.5	--------
Labridae (wrasses)	8	3	.3	5.0	--------
Champsodontidae	2	2	.2	6.0	--------
Bleniidae (blennies):					
Petroscirtes sp	29	10	.9	29.5	--------
Unidentified blennies	21	3	.3	12.0	--------
Acanthuridae (surgeonfishes)	1,067	184	16.8	1,007.2	1.9
Gempylidae (snake mackerels):					
Gempylus serpens	1	1	.1	9.0	--------
Unidentified snake mackerels	84	49	4.5	534.0	1.0
Scombridae (tunas and mackerels):					
Katsuwonus pelamis (skipjack)	19	16	1.5	2,668.0	5.1
Neothunnus macropterus (yellowfin)	1	1	.1	820.0	1.6
Parathunnus sibi (big-eyed tuna)	2	2	.2	270.0	.5
Unidentified tunas	34	24	2.2	1,093.5	2.0
Nomeidae (rudderfishes)	1	1	.1	2.0	--------
Bothidae (flatfishes)	1	1	.1	1.0	--------
Echeneidae (remoras):					
Remora remora	16	15	1.4	123.0	.2
Unidentified remoras	5	4	.4	31.0	--------
Balistidae (triggerfishes):					
Balistes ringens	45	24	2.2	570.5	1.1
Unidentified triggerfishes	322	91	8.3	698.0	1.3
Monacanthidae (filefishes)	24	16	1.5	49.0	.1
Ostraciidae (trunkfishes):					
Ostracion diaphana	137	75	6.8	349.5	.7
O. lentiginosus	1	1	.1	4.0	--------
Unidentified trunkfishes	215	84	7.7	223.5	.4
Tetrodontidae (puffers):					
Sphaeroides lagocephalus	14	11	1.0	768.0	1.5
Unidentified puffers	10	12	1.1	133.0	.3
Diodontidae (porcupinefishes)	8	8	.7	81.0	.2
Molidae (headfishes):					
Ranzania truncata	1	1	.1	520.0	1.0
Unidentified fish and fish remains	2,439	529	48.2	4,204.1	8.0
Total	--------	--------	--------	52,336.1	--------

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[1] Given only when 0.1 percent or greater.

RESULTS

FOOD HABITS OF THE YELLOWFIN TUNA

Detailed data obtained during this study are presented in table 3. This table incorporates the combined data for all stomachs examined and serves as a checklist of the food organisms identified. It is apparent from table 3 and figure 3 that the food of the 1,097 yellowfins sampled was composed by volume almost entirely of fish (46.7 percent), squid (26.2 percent), and crustaceans (24.8 percent). The small remainder consisted of pelagic tunicates (0.6 percent) and molluscs other than squid (1.7 percent). Representatives of 38 fish families and 11 major invertebrate groups were found in the stomach contents. Despite the great variety of organisms only a few items were of primary importance in the diet of the yellowfin. Those food elements ranking large in number, volume, and frequency of occurrence were crab larvae, stomatopod larvae, squid, pomfrets (Bramidae), and surgeonfish (Acanthuridae). Fishes such as flyingfish (Exocoetidae), mackerel scad (*Decapturus* sp.), and skipjack (*Katsuwonus pelamis*) were relatively important in volume because of their large individual size, but ranked low in number and frequency of occurrence, indicating that they were only occasionally utilized.

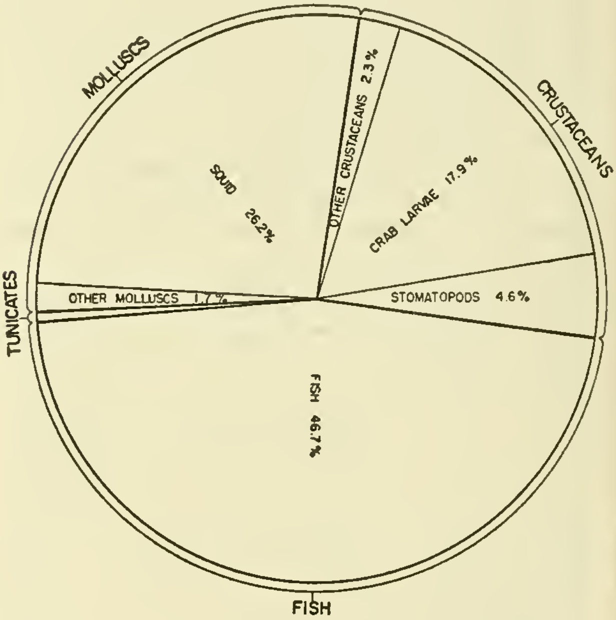

FIGURE 3.—The comparative importance of the major food categories for the 1,097 sampled yellowfin (as percent of total volume).

Size of organisms taken

More than 75 percent of the stomachs examined contained organisms individually displacing less than 0.5 cc. The regular occurrence of larval and postlarval crustaceans, and the occasional record of small heteropods and pteropods indicate a consistent tendency for the tuna to take organisms of very small size.

The maximum size of organisms used for food is dependent on the size of the tuna. Some stomachs were distended by large carangid and scombroid fishes. Certain elongate fishes such as the alepisaurids and snake mackerels were folded two or three times in the stomach. One stomach from a yellowfin (1,358 mm. fork length) contained a skipjack, *Katsuwonus pelamis*, exceeding 400 mm. in length, and vertebral remains found during the study suggest that prey of this size is not uncommon. The maximum size of food organisms, estimated from these data, is approximately one-third the length of the yellowfin.

Gorging

Observers aboard the *John R. Manning* reported an aggregation of crab megalops in the vicinity of Christmas Island (Line Island Group) on May 12 and 13, 1950. The larvae were so numerous that the screened intake of the heat exchanger for the vessel's engines became clogged and had to be cleaned on several occasions. Stomachs were preserved from 21 yellowfin, ranging from 879 to 1,365 mm. fork length, captured in the vicinity at this time. All contained crab larvae as the principal food component, averaging 1,500 larvae (180 cc.) per stomach. Many fish were gorged and regurgitated large amounts of the larvae when they were landed.

Diurnal variation

The time of capture is known for 660 yellowfin caught at the surface. Of these, 398 yellowfin landed between 6 a. m. and 12 m. had an average stomach-content volume of 22.1 cubic centimeters; 74 of the 398 fish had empty stomachs. The average volume of stomach contents of 258 yellowfin landed between 12 m. and 6 p. m. was 49.7 cubic centimeters; of this number, 14 had empty stomachs. These results indicate that the yellowfin sampled were not necessarily night feeders, as sometimes reported (Ban 1941), but that they had definitely been feeding during the day and probably right up to the time of capture. These data are based primarily on small and medium-sized yellowfin, all surface-caught fish; consequently, the implications may possibly not apply to yellowfin in general.

Variation in volume of stomach contents

Table 4 shows the distribution of stomach-content volumes according to an arbitrary scale devised by the authors. The large percentage of empty or almost empty stomachs is surprising, but may be related to the rate of digestion or feeding habit. It is difficult to believe that the food volumes of less than 25 cc. which were found in 58 percent of the yellowfin examined represent an average daily ration for these large, fast-moving fish. We conclude that the rate of digestion is very rapid or that the fish must depend largely on occasional opportunities to gorge.

The frequency of empty stomachs and of volumes less than 3 cc. appears to vary considerably among the catches obtained by the three fishing methods. The high percentage of empty stomachs among the pole-and-line-caught yellowfin may be the result of these fish coming from surface schools, whereas there are indications that the catch for the other two fishing methods was not from well-defined schools but rather was composed of individual fish or of fish from small congregations. Also, the different fishing methods, by taking fish

TABLE 4.—*Distribution of the volume of stomach contents from 1,097 yellowfin tuna, for each fishing method and for all methods combined*

Volume of stomach contents	Troll caught			Pole-and-line caught			Longline caught			Total		
	Number	Percent	Accumulated percent	Number	Percent	Accumulated percent	Number	Percent	Accumulated percent	Number	Percent	Accumulated percent
Empty [1]	35	7.3	7.3	61	20.0	20.0	5	1.6	1.6	101	9.2	9.2
0.1 to 2.9 cc	118	24.6	31.9	33	10.8	30.8	9	2.9	4.5	160	14.6	23.8
3.0 to 9.9 cc	125	25.9	57.8	46	15.1	45.9	28	9.1	13.6	199	18.1	41.9
10.0 to 24.9 cc	80	16.6	74.4	39	12.8	58.7	61	19.6	33.2	180	16.4	58.3
25.0 to 49.9 cc	37	7.7	82.1	33	10.8	69.5	74	23.8	57.0	144	13.1	71.4
50.0 to 99.9 cc	28	5.8	87.9	62	20.3	89.8	61	19.6	76.6	151	13.8	85.2
100.0 to 199.9 cc	34	7.1	95.0	27	8.9	98.7	47	15.1	91.7	108	9.8	95.0
200.0 to 499.9 cc	21	4.4	99.4	4	1.3	100.0	22	7.1	98.8	47	4.3	99.3
500.0 to 999.9 cc	2	0.4	99.8	----------	----------	----------	4	1.3	100.0	6	0.5	99.8
1,000 cc and more	1	0.2	100.0	----------	----------	----------	----------	----------	----------	1	0.1	99.9
Total	481	100.0	----------	305	100.0	----------	311	100.0	----------	1,097	99.9	----------

[1] Less than 0.1 cc.

of somewhat different size groups and from different habitats, may influence the average volume of stomach contents.

In general, there was an increase in the mean food volume with an increase in the fork length of the fish (table 5, fig. 4). The average stomach content per unit of body weight (cc./lb.) was found to decrease, however, as the weight of the fish increased (fig. 5). Except for possible aberrancies at the extreme ends of the polygons and in the 1,250-mm., approximately 84-lb., group, which may be due to quirks of sampling, there appears to be a rectilinear relation between the volume of stomach contents and size of the fish.

The great variation in volume of stomach contents is illustrated in table 5. For the various size groups represented, the standard deviation (s) is roughly proportional to the mean volume ($\bar{x}$), indicating a great increase in variance, or variation about the mean, of volume of stomach contents with increase in fork length. This variation is related to the fact that large yellowfin eat organisms of greater dimension than those consumed by small yellowfin, but that both groups feed on the same minute organisms, such as crab and stomatopod larvae. Therefore, the larger the yellowfin the greater the size range of the individual food elements and the greater the range in volume of stomach contents that may be expected.

Variation in food of yellowfin related to locality, habitat, and body size

As indicated in tables 1 and 2 and figure 1, yellowfin were captured by three methods, came from different depths and localities, and covered a wide size range. It was difficult, therefore, to find within this heterogeneous lot of fish, groups that might be compared to show differences resulting from the action of a single variable.

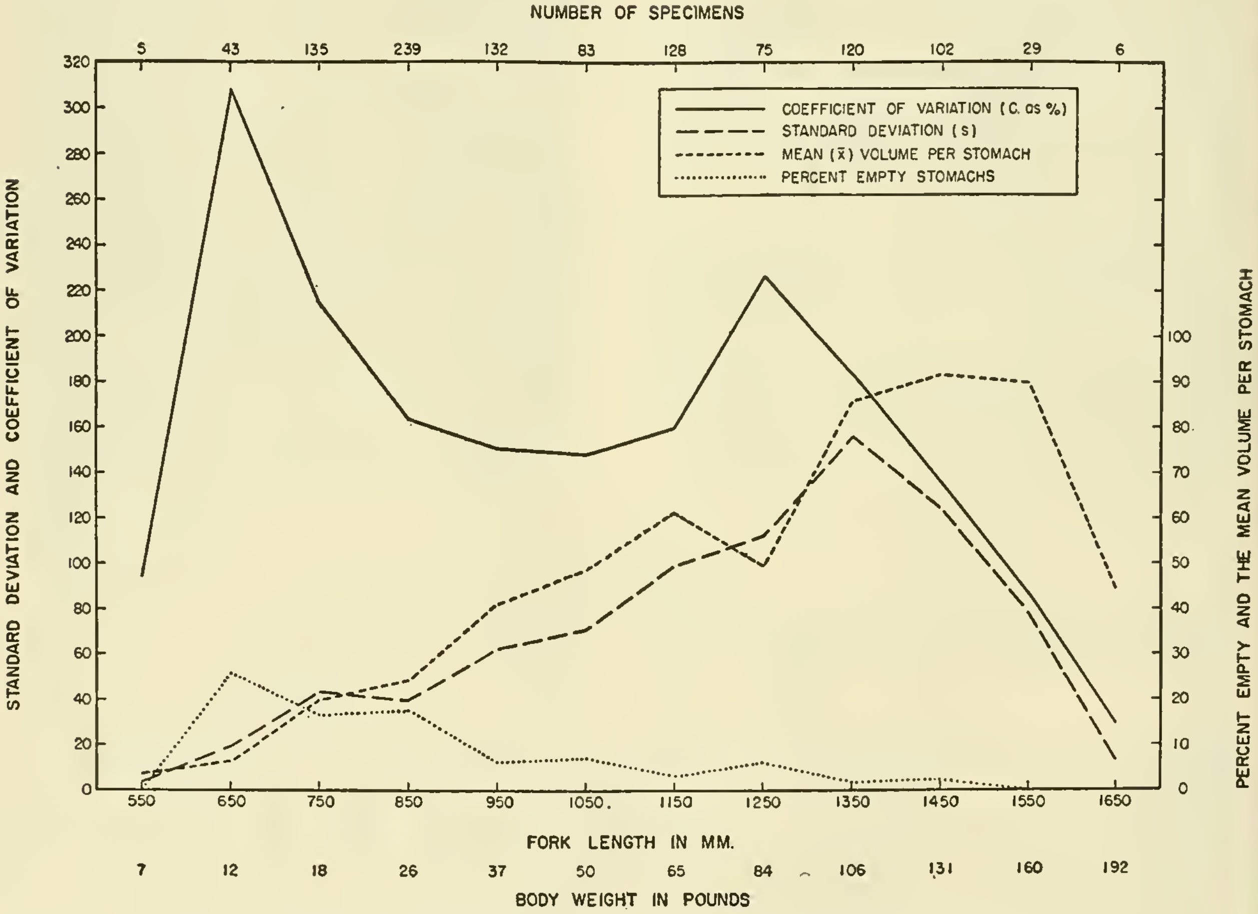

Figure 4.—Relation of percent of empty stomachs, mean volume of food per stomach, standard deviation, and coefficient of variation for volumes of stomach contents to body size of 1,097 yellowfin tuna.

TABLE 5.—*Relation between size and volume of stomach contents of yellowfin tuna*

N=total number of sampled fish for each size group
Empty=number of empty stomachs
x̄=mean, or average food volume per stomach
s=standard deviation, indicating variation in food volume for each size class
C=the coefficient of variation, an index to variability

Variation in volume of stomach contents	For size class (fork length in millimeters) of—												Total
	500–599	600–699	700–799	800–899	900–999	1000–1099	1100–1199	1200–1299	1300–1399	1400–1499	1500–1599	1600 1699	
Troll caught:													
N	5	30	88	98	102	63	63	14	12	5	1	--------	481
Empty	0	2	11	7	7	5	1	1	0	1	0	--------	35
Percent empty	0	6.7	12.5	7.1	6.9	7.9	1.6	7.1	0	20	0	--------	--------
x̄	3.7	8.6	12.0	15.9	37.0	50.8	77.1	19.4	199.1	86.3	--------	--------	--------
s	3.5	24.2	30.6	30.7	62.4	77.9	126.0	19.9	376.3	114.6	--------	--------	--------
C (percent)	94.1	281.4	255.0	103.1	168.6	153.3	163.4	102.6	189.0	132.8	--------	--------	--------
Pole-and-line caught:													
N	--------	13	47	141	26	8	40	18	10	1	1	--------	305
Empty	--------	9	11	35	1	1	1	1	1	1	0	--------	61
Percent empty	--------	79.2	23.4	24.8	3.8	12.5	2.5	5.6	10.0	100.0	0	--------	--------
x̄	--------	0.8	35.0	30.3	60.9	51.6	35.5	42.7	76.3	--------	--------	--------	--------
s	--------	1.5	57.2	44.2	62.3	47.1	30.4	32.8	77.8	--------	--------	--------	--------
C (percent)	--------	187.5	163.4	145.9	102.3	91.3	85.6	76.8	102.0	--------	--------	--------	--------
Longline caught:													
N	--------	--------	--------	--------	4	12	25	43	98	96	27	6	311
Empty	--------	--------	--------	--------	0	0	2	2	1	0	0	0	5
Percent empty	--------	--------	--------	--------	0	0	8.0	4.7	1.0	0	0	0	--------
x̄	--------	--------	--------	--------	12.9	29.2	61.7	62.2	72.5	92.7	85.8	44.2	--------
s	--------	--------	--------	--------	4.7	35.2	79.9	145.5	108.3	125.5	75.2	12.8	--------
C (percent)	--------	--------	--------	--------	36.4	120.5	129.5	233.9	149.4	135.4	87.6	29.0	--------
All methods combined:													
N	5	43	135	239	132	83	128	75	120	102	29	6	1,097
Empty	0	11	22	42	8	6	4	4	2	2	0	0	101
Percent empty	0	25.6	16.3	17.6	6.1	7.2	3.1	5.7	1.7	2.0	0	0	--------
x̄	3.7	6.2	20.0	24.4	41.0	47.7	61.1	40.5	85.5	91.5	89.9	44.2	--------
s	3.5	19.1	43.1	39.8	62.1	70.7	97.8	112.3	156.7	124.2	78.3	12.8	--------
C (percent)	94.1	308.1	215.5	163.1	151.5	148.2	160.1	226.9	183.3	135.7	87.1	29.0	--------

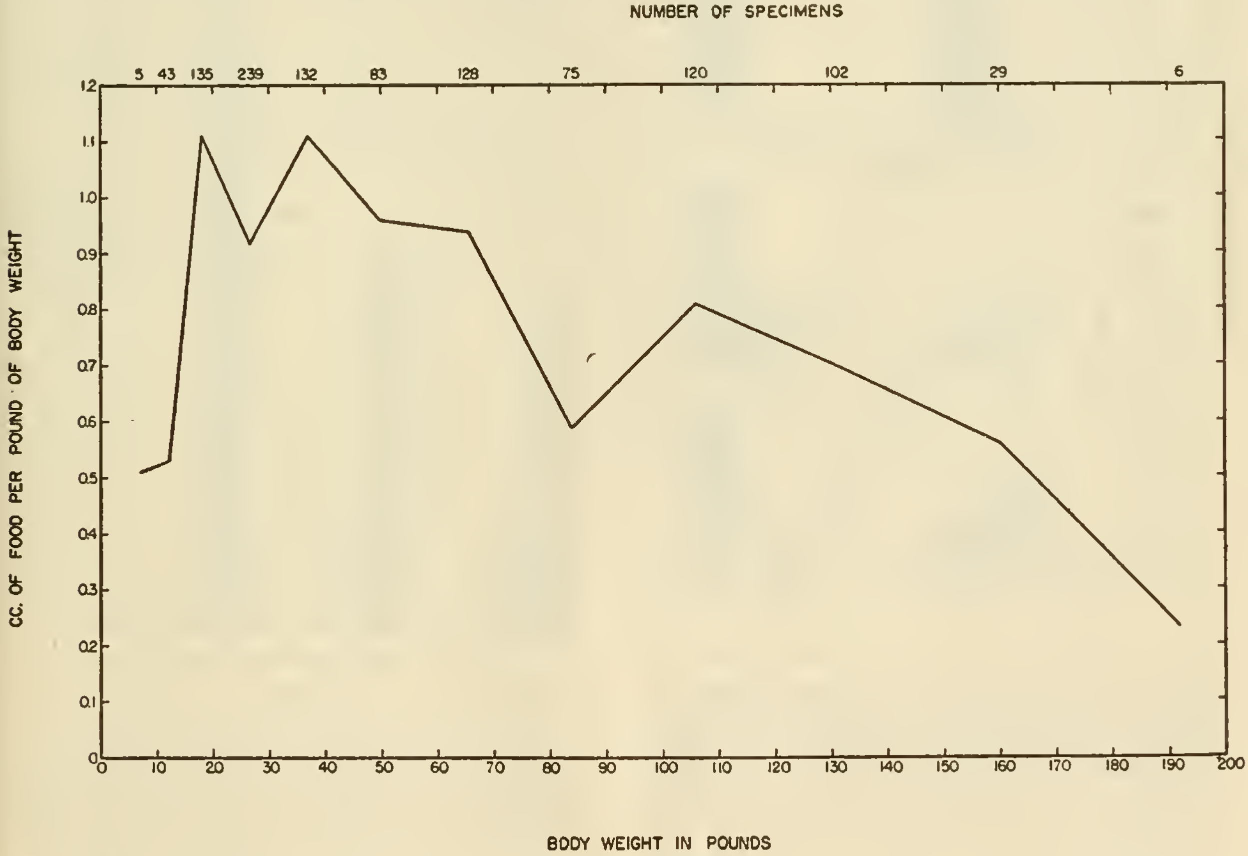

FIGURE 5.—Relation of stomach contents per unit body weight (cc./lb.) to body weight of 1,097 yellowfin tuna.

To investigate differences between localities, we may compare the food of yellowfin of 1,000 to 1,299 mm. fork length (approximately 43 to 92 lb.), captured in the Line Islands, with the food of a group of the same size range from the Phoenix Islands. In figure 6, we used average volume per stomach for each of the major food groups as an index to the availability of those organisms in each locality. As shown in figure 6, the most apparent locality differences lay in the proportionately greater average volume of crab larvae (megalops) found in the Line Island yellowfin, at least in respect to the surface-caught fish, and the greater average volume of fish in the Phoenix Island yellowfin. During the 2-year period covered by this study, we failed to encounter in the Phoenix Islands any swarms of crab larvae such as occurred in the Line Islands during May and June, 1950 and 1951. The data indicate that locality differences may be of considerable importance and should be considered in an evaluation of the food of the yellowfin.

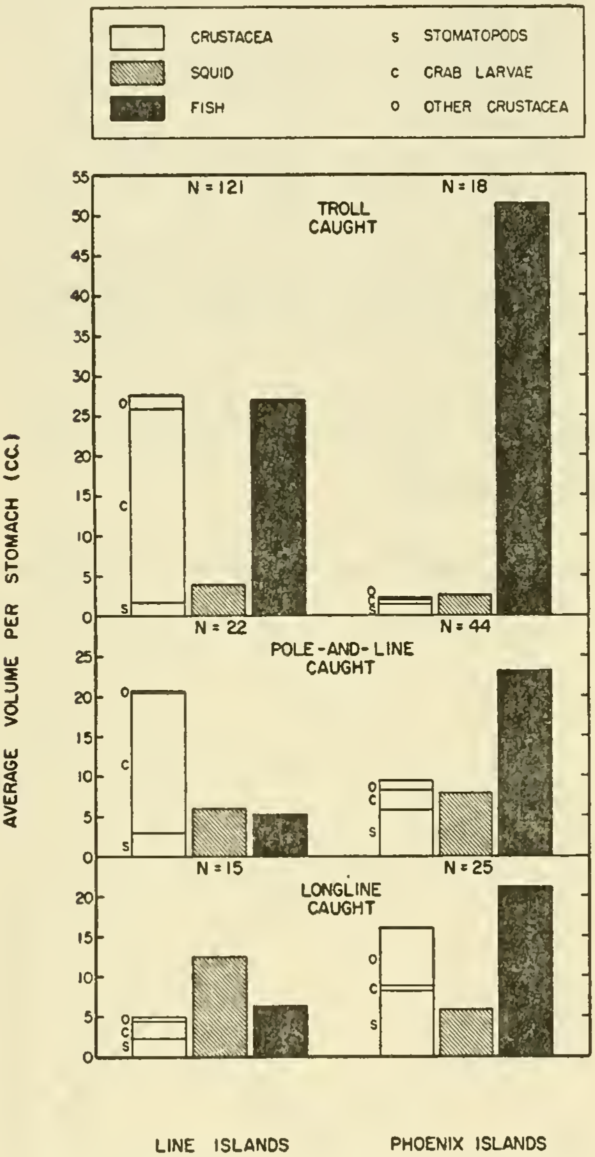

Figure 6.—Differences in availability of the major food categories between the Line and Phoenix Islands, as indicated by average volume per stomach, for yellowfin 1,000 to 1,299 mm. fork length. The troll- and pole-and-line-caught fish were captured within 10 miles of land; the longline fish within 25 miles of land. N = number of stomachs.

Not only are differences in the availability of food organisms between localities evident (fig. 6), but also between lots of fish taken by different fishing methods, i. e., fish from different habitats or depths within an area. To examine the influence of habitat on the composition of the food, we may compare the same six lots of fish, using the percentage of total volume as a measure of importance for each food group (fig. 7). The localities were treated separately, since we had found that locality differences did exist. Figure 7 indicates that there was great variation in food composition between similar habitats from different localities, and also for different habitats within localities. The only apparent consistent relationship is that the proportion of stomatopods was higher in the subsurface-caught (longline) fish than in the surface-caught (troll and pole-and-line) fish.

Figure 8 demonstrates the variation in availability of the major food groups in relation to distance the tuna was captured from land. Since fish taken at the surface came almost entirely from inshore regions, the major data available for this comparison are those from the longline-caught fish. For both size groups of yellowfin, 1,299 mm. or less and 1,300 mm. or more, the average volume of crustacea per stomach was much greater for the fish taken near land (0 to 24 miles from shore) than for those from offshore areas. The crustacean fraction changed not only in its average volume, but also in its composition; i. e., for the near-shore region it was composed predominantly of crab and stomatopod larvae, whereas for the offshore region it consisted of pelagic amphipods and shrimps. Squid and fish were staple foods in all environments, although the former was consistently higher in average volume in the larger yellowfin.

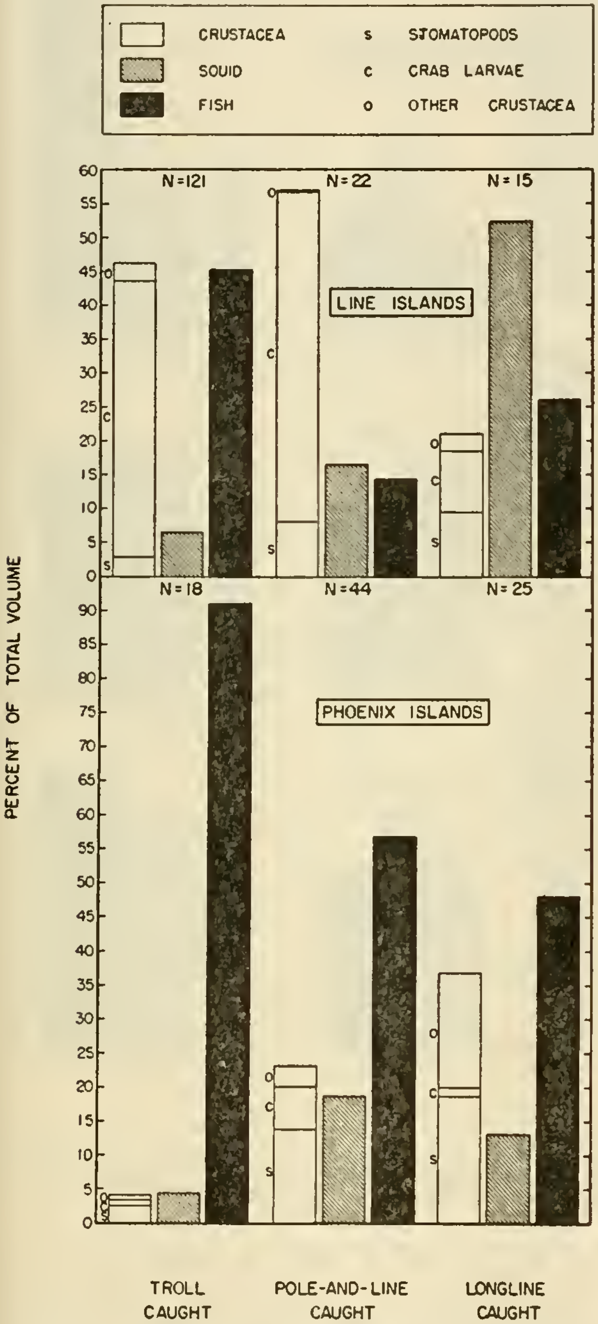

FIGURE 7.—Differences in the composition of the food of yellowfin (1,000–1,299 mm. fork length) with method of capture, for two general localities. The troll- and pole-and-line-caught fish were captured within 10 miles of land, the longline-caught fish within 25 miles of land. N=number of stomachs.

As in the crustacea, there were differences in the kinds of fish found in the food of yellowfin from different environments. Fish families commonly occurring in stomachs of the near-shore yellowfin were Balistidae, Acanthuridae, and Carangidae. For the offshore yellowfin, representatives of Bramidae, Exocoetidae, and Gempylidae were more prevalent in the food. The food of 11 troll-caught yellowfin captured more than 10 miles from land consisted of 57 percent fish, 42 percent squid, and about 1 percent crustacea, the average volumes per stomach being, respectively, 32.3, 23.8, and 0.6 cc.

From the beginning of the study it was obvious that not only the volume of stomach contents but also the composition of the food varied with the size of the yellowfin. While the same foods were eaten by both large and small tuna, they were not consumed in the same proportions. Since large, medium, and small yellowfin were taken by surface fishing from the same coastal areas, we assume that they had equal opportunity to feed on a common source of food organisms. The differences in stomach contents may be due either to a change in food preference or to the ability to catch and swallow certain organisms as the tuna increases in size. Figure 9 shows the variation in the three major food categories with increase in size of yellowfin. The most marked differences are the low percentage of crustacea and the high percentage of fish in the large surface-caught yellowfin, and the apparently greater importance of squid in the food of small and medium-sized yellowfin. As all but 2 percent of the surface-caught fish were taken less than 10 miles from land, the variation in the size of the yellowfin tuna captured appears to be the greatest variable. Table 6 summarizes the stomach contents of 775 of the 781 fish taken by surface fishing. The data arranged in arbitrary size categories show that the stomachs of the smaller fish contained more crustacean elements and fewer fish than did those of the larger specimens. Squid are a relatively unimportant fraction in all sizes of fish caught near land at the surface. On the other hand, longline-caught (subsurface) yellowfin tuna were mostly larger fish and showed little variation in size; however, the locality of capture, in reference to distance from land, did vary greatly. Table 7 summarizes the stomach contents of 311 fish taken well below the surface by longline fishing.

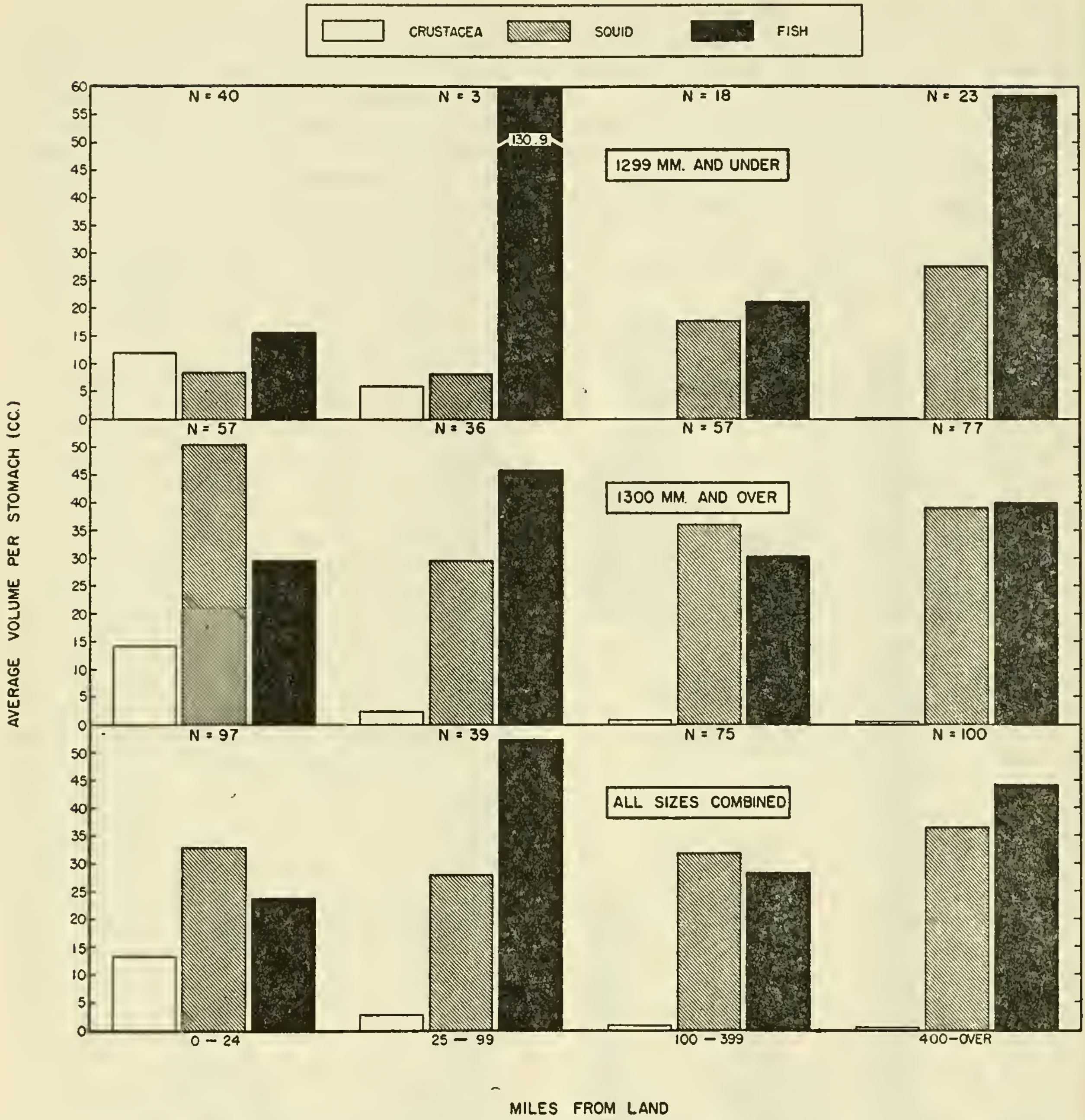

FIGURE 8.—Variation in availability of the major food categories with distance from land, for longline-caught yellowfin, as indicated by average volume per stomach. N = number of stomachs.

Relation of volume of stomach contents to oceanographic conditions

On cruise 11 of the *Hugh M. Smith*, longline fishing was conducted at a series of stations along 150° W. longitude, ranging from about 15° N. to 5° S. latitude. A single oblique plankton haul to a depth of 200 meters was made daily at each station. The volume of zooplankton at each station, expressed in cubic centimeters for each cubic meter of water strained, and the catch of yellowfin per 100 hooks fished at each station are given in figure 10. For purposes of comparison the cruise area may be divided into (1) An area of poor tuna catch, north of 6° N. latitude; (2) an area of good tuna catch at 6° to 4° N. latitude; (3) another area of good catch at 3° to

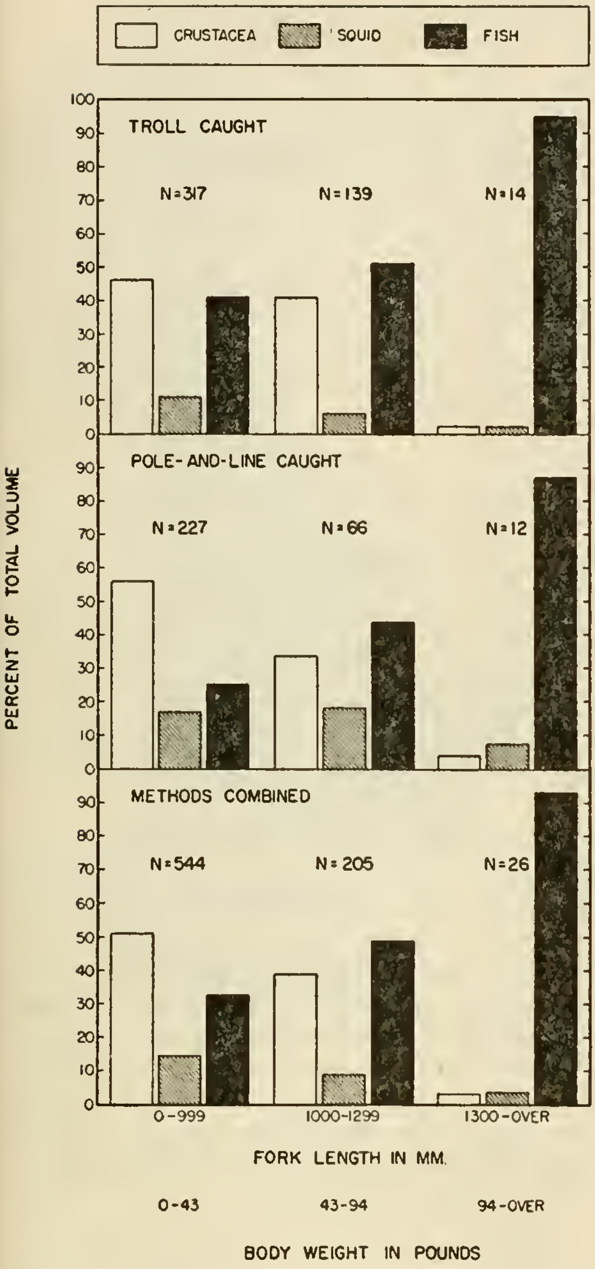

Figure 9.—Variation in food composition with body size for yellowfin captured at the surface within 10 miles of land. N = number of stomachs.

1° N. latitude; and (4) an area of poor catch, from the Equator to 5° S. latitude. Fishing was done at stations 1 and 3, but no yellowfin were captured. The number of yellowfin captured in each of these areas, the number of stomachs examined, and the average volume of food in each stomach are shown in figure 10.

North of the Equator the yellowfin catch varied generally with zooplankton volumes, but south of the Equator the catch dropped off markedly while the zooplankton population persisted at a relatively high level. The few yellowfin captured south of the Equator were well fed, however, as indicated by the relatively high volume of food found in their stomachs.

Previous cruises of the *Hugh M. Smith* have demonstrated the existence of a "rich zone" in the region of the Equator that has been considerably higher in chemical nutrients and zooplankton than waters to the north or south (Cromwell 1951, King and Demond 1953). On most crossings of the equatorial region, the rich zone was found between the Equator and 4° to 5° N. latitude. On occasion, however, perhaps because of certain peculiar conditions of winds and currents, the rich zone was found to be displaced three or four degrees to the southward with the general pattern of relative zooplankton distribution remaining as in figure 10. It may be that for the greater part of the year the region of greatest productivity conforms more nearly to the distribution of the yellowfin catch of cruise 11 than to the distribution of zooplankton abundance. The latter may be more transitory in position than the fish population.

DISCUSSION

The 1,097 yellowfin upon which this study is based represent slightly more than 20 percent of all yellowfin captured during experimental and exploratory fishing in 1950 and 1951 by vessels of the Pacific Oceanic Fishery Investigations. The fish were captured by three standard commercial fishing methods: longline or flagline fishing, pole-and-line fishing with live bait, and surface trolling with artificial lures. The yellowfin caught on longlines averaged approximately 125 pounds in weight and were captured well below the surface both near and away from land; the fish caught by pole-and-line were taken near shore at the surface and averaged less than 30 pounds; and the fish caught by trolling were all taken at the surface, most of them near shore (less than 2 percent were taken more than 10 miles from land), and averaged approximately 30 pounds.

There are two possible explanations for this marked variation in results obtained by the different fishing methods. First, the fishing methods

TABLE 6.—*Surface-caught yellowfin tuna, localities combined: stomach-content analysis of 775 fish*

Fork length and method of capture	Number of stomachs	Stomatopods		Crab larvae		Other crustaceans		Squid		Other molluscs		Tunicates		Fish	
		Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent cf total volume	Average volume (cc.)	Percent of total volume
Less than 1,000 mm.:															
Trolling	317	2.2	11.1	6.0	29.7	1.0	5.2	2.3	11.2	0.1	0.7	0.2	0.9	8.3	41.2
Pole-and-line	227	2.1	6.4	16.0	48.6	.3	.1	5.6	17.1	.5	1.5	.1	.2	8.3	25.3
Combined	544	2.2	2.2	8.6	39.8	.7	2.9	3.7	14.4	.3	1.1	.1	.2	8.3	32.6
1,000 to 1,299 mm.:															
Trolling	139	1.6	2.7	21.2	35.7	1.5	2.5	3.7	6.3	.2	.4	.8	1.4	30.2	50.9
Pole-and-line	66	4.8	12.2	7.5	19.1	.9	2.3	7.1	18.1	1.5	3.9	.3	.7	17.2	43.7
Combined	205	2.6	5.0	16.8	31.7	1.3	2.5	4.8	9.1	.7	1.3	.6	1.2	26.0	49.2
Over 1,300 mm.:															
Trolling	14	.6	.3	4.1	2.1	--------	--------	4.9	2.5	--------	--------	.7	.4	187.4	94.8
Pole-and-line	12	1.4	2.1	.5	.8	.9	1.4	5.2	7.6	.4	.6	.1	.2	59.2	87.3
Combined	26	1.0	.7	2.4	1.8	.4	.3	5.0	3.6	.2	.1	.4	.3	128.2	93.1

TABLE 7.—*Subsurface-caught yellowfin tuna, size groups combined: stomach-content analysis of 311 fish*

Distance from land	Number of stomachs	Stomatopods		Crab larvae		Other crustaceans		Squid		Other molluscs		Tunicates		Fish	
		Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volumo	Average volume (cc.)	Percent of total volume	Average volume (cc.)	Percent of total volume
0 to 24 miles	97	6.5	9.1	2.9	4.1	3.9	5.5	33.1	46.1	0.8	1.2	0.6	0.8	23.8	33.3
25 to 99 miles	39	.2	.2	--------	--------	2.5	3.0	28.1	33.4	.4	.5	.3	.4	52.4	62.4
100 to 399 miles	75	.1	.2	.1	.1	.5	.8	31.9	51.2	1.2	1.9	.1	.2	28.3	45.5
400 miles and over	100	--------	--------	.3	.4	.2	.2	36.5	42.9	3.8	4.4	.1	.1	44.2	52.0

as employed by our vessels may be selective. Surface trolling and live-bait fishing appear to be more effective near land than away from land, and in the central Pacific they take small and medium-sized fish. Longline fishing, in contrast, is effective both near and away from land, but the catch is composed almost exclusively of medium-sized and large fish. On the other hand, the distribution of the fish may actually be in accordance with the catch; i. e., large fish scarce in surface waters both offshore and near shore but more abundant at subsurface levels; small fish occurring most abundantly in surface waters near shore, uncommonly in surface waters offshore, and rarely in subsurface waters, whether offshore or near shore; and medium-sized fish existing throughout the ranges of both the smaller and the larger fish.

As the collection of stomach material was just one of several objectives of each fishing cruise, it was not possible to schedule the trips so as to yield samples evenly distributed in time for each major area and habitat. For example, pole-and-line fishing was conducted only during January and July 1950 and June 1951. Longline fishing was done near Canton Island (Phoenix Group) in July 1950, and in the general area of the Line Islands in November 1950 and September 1951. Surface trolling was done on all cruises but, as previously stated, yielded few fish from waters 10 miles or more from land. It is apparent, therefore, that while our samples were rather homogeneous within themselves, they differed in time and area of capture, habitat, average size, and in other ways. Consequently any comparisons between different lots of fish must be qualified with respect to these different factors.

According to Ricker (1946), fish are usually classified as bottom feeders, plankton eaters, or fish eaters. From the results of this study it is apparent that maturing and adult yellowfin of the central Pacific feed on macrozooplankton, fish, and also pelagic cephalopods. In addition to the great variety in the food, it is surprising to discover that small organisms of 0.2 to 0.5 cc. in volume are regular prey of these large, fast-moving fish.

Since crustacean larvae were so prominent in the food of those small yellowfin sampled, the question arises as to whether the apparent greater

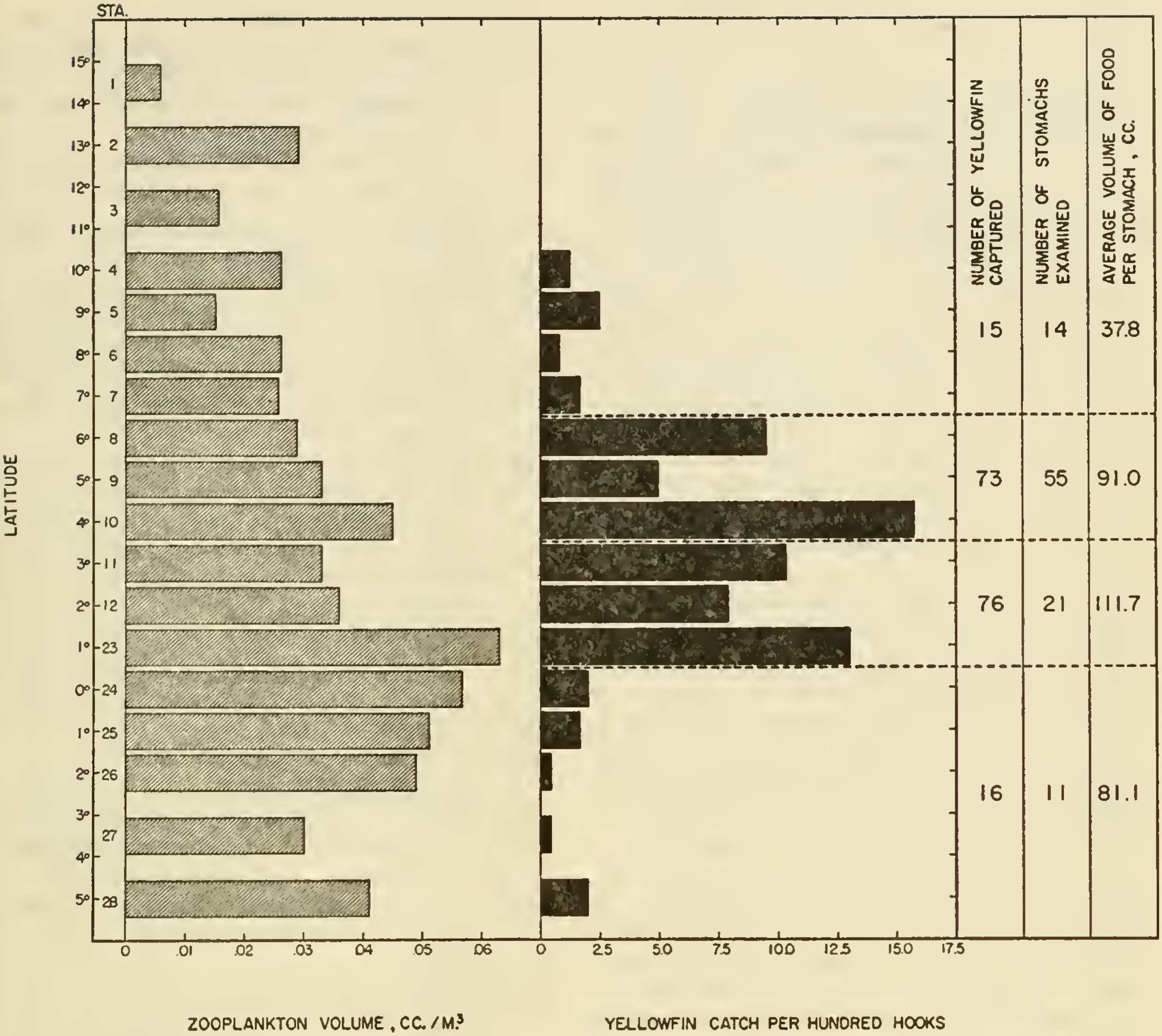

FIGURE 10.—Relation of zooplankton abundance, yellowfin catch per hundred hooks, and average volume of food per stomach as found on cruise 11 of the *Hugh M. Smith* along 150° W. longitude for the range of latitudes indicated.

abundance of these fish near land is related to the greater abundance of crustacean larvae in such areas. Is the distribution of the fish dependent upon the availability of these food elements? These questions cannot be answered from the results of this study, but they will be the objectives of future research.

Ricker (1946) states that with few exceptions large fish more often have empty stomachs than do smaller ones of the same species. Our observations (table 5) indicate that just the reverse may be true for the yellowfin. Ricker states also that the average stomach content per unit of body weight is less among large fish, which is in general agreement with the results of this investigation (fig. 5).

There is some evidence that the rate of feeding in fishes is directly proportional to the availability of food. Therefore, in view of the average fisherman's belief that more tuna "feed" is found near the reefs than offshore in the open ocean, it was surprising to find that for comparable size groups the fish taken offshore contained on the average the same quantity of food in their stomachs as the fish taken near land (table 7). Also, fish from the subsurface contained as much food as those from the surface.

Although we believe this report provides the most complete information available on the food of the yellowfin, the more important observations in other areas (Kishinouye (1917, 1923) for the Bonin Islands and general western Pacific; Nakamura (1936) for the Celebes Sea; Marukawa (1939) and Ban (1941) for the equatorial western Pacific; Kanamura and Yazaki (1940a, 1940b) and Ronquillo (1950) for the Philippines; Herald (1949) and Welsh (1949) for the eastern Pacific and Hawaiian Islands) and those reported here are in general agreement on the chief constituents of the food of the yellowfin. The number and kind of individual species listed may vary with the locality and the extensiveness of the work done. A summary of the species taken shows that yellowfin have an extremely varied diet and feed to a large extent not only on reef fauna but also on organisms of the open ocean, both plankton and nekton. Since most pelagic crustaceans, molluscs, and fish, within rather broad size limits, appear to be acceptable as food, the distribution and abundance of maturing and adult yellowfin are most probably not determined by the occurrence of specific food items, but rather are influenced by the total amount of food present in an area.

The food of juvenile yellowfin is yet to be investigated. Whereas the adults accept a wide variety of food, the juveniles may be more specific in their feeding habits. In such a case, the abundance of a particular food or foods could have an important influence on the survival and growth of the young. Few yellowfin less than 400 mm. (about 2.8 lb.) are taken by present fishing methods.

Also there remains the problem of evaluating the abundance of tuna food organisms in different areas and at different depths to determine which regions of the Pacific may potentially support the greatest populations of tuna. This phase of the problem, however, awaits the development of effective gear for quantitative sampling.

SUMMARY

1. This study is based on the quantitative analysis of the stomach contents of 1,097 yellowfin tuna (*Neothunnus macropterus*) taken in the central Pacific.
2. The fish were captured by three fishing methods, trolling, pole-and-line, and long-line, came from varying habitats, onshore and offshore, surface and subsurface, and were of different size groups.
3. The 1,097 stomachs contained a total volume of 52,336.1 cc. of food, of which 47 percent by volume was fish, 26 percent squid, and 25 percent crustaceans.
4. Yellowfin appear to accept a great variety of animal food, and take advantage of whatever is most plentiful in the area at the time.
5. They feed on very small plankton organisms as well as large squid and fish one-third the length of the tuna.
6. Yellowfin captured in the afternoon by trolling and live-bait fishing had more food in their stomachs and fewer empty stomachs than those captured in the morning; therefore, feeding must take place during daylight hours.
7. The yellowfin taken at the surface had been feeding primarily on crustacean larvae and fish, the fish taken beneath the surface on fish and squid.
8. The yellowfin taken near land had fed on fish, crustacean larvae, and squid; those caught away from land on fish and squid.
9. Small yellowfin fed preponderantly on crustacean larvae; medium-sized yellowfin fed on fish, crustacean larvae, and squid; while the large yellowfin fed mainly on fish and squid.
10. Yellowfin from offshore areas contained as much food in their stomachs as those captured just off the reef, and they fed at subsurface levels as well as at the surface.
11. The average volume of stomach contents was (cruise 11, *Hugh M. Smith*) roughly proportional to the concentration of zooplankton in the area in which the fish were captured, i. e., the yellowfin tuna captured in the rich zone near the Equator contained greater amounts of food—zooplankton, forage fish, and squid—than those captured at more northerly or southerly latitudes.
12. Further research is needed on the food of juvenile yellowfin; on the abundance of food organisms in different areas of the Pacific and at different seasons to determine

which areas may potentially be the most productive of tuna; and on the manner of distribution of tuna in relation to the distribution of available food.

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ZOOPLANKTON ABUNDANCE IN THE CENTRAL PACIFIC

By Joseph E. King and Joan Demond

March 3, 1849

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ZOOPLANKTON ABUNDANCE IN THE CENTRAL PACIFIC

By **Joseph E. King**, *Fishery Research Biologist*, and
Joan Demond, *Fishery Aid*

The Pacific Oceanic Fishery Investigations is authorized and directed to gather information which will ensure the maximum development and utilization of the high-seas fishery resources of the United States territories and island possessions in the tropical and subtropical Pacific. One project of fundamental importance in the research program concerns the relative productivity of different areas of the sea.

Productivity has been defined by Ivlev (1945) as the "capacity of a body of water to produce a given quantity of organic matter in some particular form." A direct measurement of the "rate of production" (Clarke 1946) would require that all processes by which organic matter is built up and destroyed be known and that the rates of these processes be determined. This is difficult to do and seldom has been done even for enclosed bodies of water. In mid-ocean the difficulties are vastly greater. We believe, however, that relative productivity, or productivity as defined by Ivlev, may be estimated indirectly by measuring the amounts of basic chemical nutrients in the water and the standing crops of plankton and fish. This report considers the quantity of zooplankton, 1 of the 2 main constituents of the total plankton crop, and its relation to certain physical and chemical factors in the central Pacific environment.

Zooplankton is essential food for much of the vertebrate fauna of the sea. It is utilized both directly and indirectly by tunas (the group of fish presently under study by these investigations). Kishinouye (1924) and Imamura (1949) have shown that zooplankton is prominent in the food of juvenile tunas. A variety of zooplankton organisms has also been observed in the food of adult tunas (Kishinouye 1917; Beebe 1936; Suyehiro 1942; Clemens and Wilby 1946; Reintjes and King 1953). The bulk of the zooplankton, however, reaches the tuna indirectly, being utilized by plankton-feeding animals which are in turn eaten by the tunas.

Potential food-fish resources are likely to exist in proportion to the amount of substance available for their nutriment. When vast areas of the sea are to be investigated, the several physical, chemical, and biotic properties of water associated with the production of nutriment for fish can be more readily and reliably surveyed than the abundance of the fish themselves. This report is concerned with the zooplankton from the particular viewpoint of its usefulness as an indicator of the relative productivity of the various portions of the area covered.

The literature includes a number of papers dealing with the plankton of the tropical and subtropical Pacific. One of the most valuable of these is the report by Graham (1941) on plankton collections taken by the *Carnegie* in the eastern and central Pacific. Kramer (1906) reported on a series of collections extending from Samoa to the Marshall Islands. Jesperson (1935) described results obtained by the *Dana* while traversing a series of stations reaching from Panama to the western Pacific, south of the Equator. For the western Pacific there are the publications of Matsuya (1937), Motoda (1940), Haneda (1942), and Tokioka (1942), which deal mainly with the plankton of lagoon, bay, and coastal waters but also provide some data on offshore plankton. The several papers of Marshall (1933), Russell (1934), and Russell and Colman (1931, 1934, 1935) supply a wealth of information on the plankton of the Great Barrier Reef Lagoon, but little on oceanic plankton. The papers of Johnson (1949) on the plankton of Bikini, and Sargent and Austin (1949) on the productivity of an atoll in the northern Marshalls, also deal primarily with the lagoon environment. The California Cooperative Sardine Research Program—a cooperative undertaking of the Scripps Institution of Oceanography, the United States Fish and Wildlife Service, the California Department of Fish and Game, the California Academy of Sciences, and the Hopkins Marine Station of Stanford University—is collecting considerable information on the zooplankton of the eastern Pacific Ocean in subtropic and temperate latitudes. This organization has supplied our laboratory with copies of its unpublished data, which, when compared with our own results, show interesting differences between the zooplankton crops of the eastern and central Pacific. Reports of many of the expeditions which have entered the Pacific, such as those of the *Challenger*, the *Albatross*, and the *Meteor*, provide extensive information on the systematics and distribution of species or groups of the zooplankton, but supply little quantitative data that may be used to evaluate the zooplankton crop in the different regions visited.

The authors wish to acknowledge their indebtedness to Dr. Milner B. Schaefer,[1] under whose direction this project was initiated, and to Dr. Albert L. Tester[2] for his very valuable assistance in the statistical phases of the study and his constructive criticism of the manuscript. We are also grateful to fellow staff members and the officers and crew of the *Hugh M. Smith* for their interest and efforts in obtaining this extensive series of collections.

COLLECTION OF ZOOPLANKTON SAMPLES

AREAS SAMPLED

This study is based on 210 collections made in the central Pacific on cruises 2, 5, 7, and 8 of the United States Fish and Wildlife Service vessel *Hugh M. Smith* in 1950 and 1951. Cruise 2 was made in January and February 1950; cruise 5 in June, July, and August 1950; cruise 7 in October and November 1950; and cruise 8 in January, February, and March, 1951. Thus, there were 2 cruises (2 and 8) at a time corresponding to the northern winter season, and 1 cruise each (5 and 7) for summer and autumn. The approximate locations of the stations are shown in figures 1a and 1b, and more exact positions are given in tables 1, 2, 3, and 4. The data are distributed in 7 long north-south sections, 6 of which cross the Equator, and in a number of shorter series of stations (cruise 8).

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[1] Formerly chief, Section of Research and Development, Pacific Oceanic Fishery Investigations; presently director of Investigations, Inter-American Tropical Tuna Commission.

[2] Professor of Zoology, University of Hawaii.

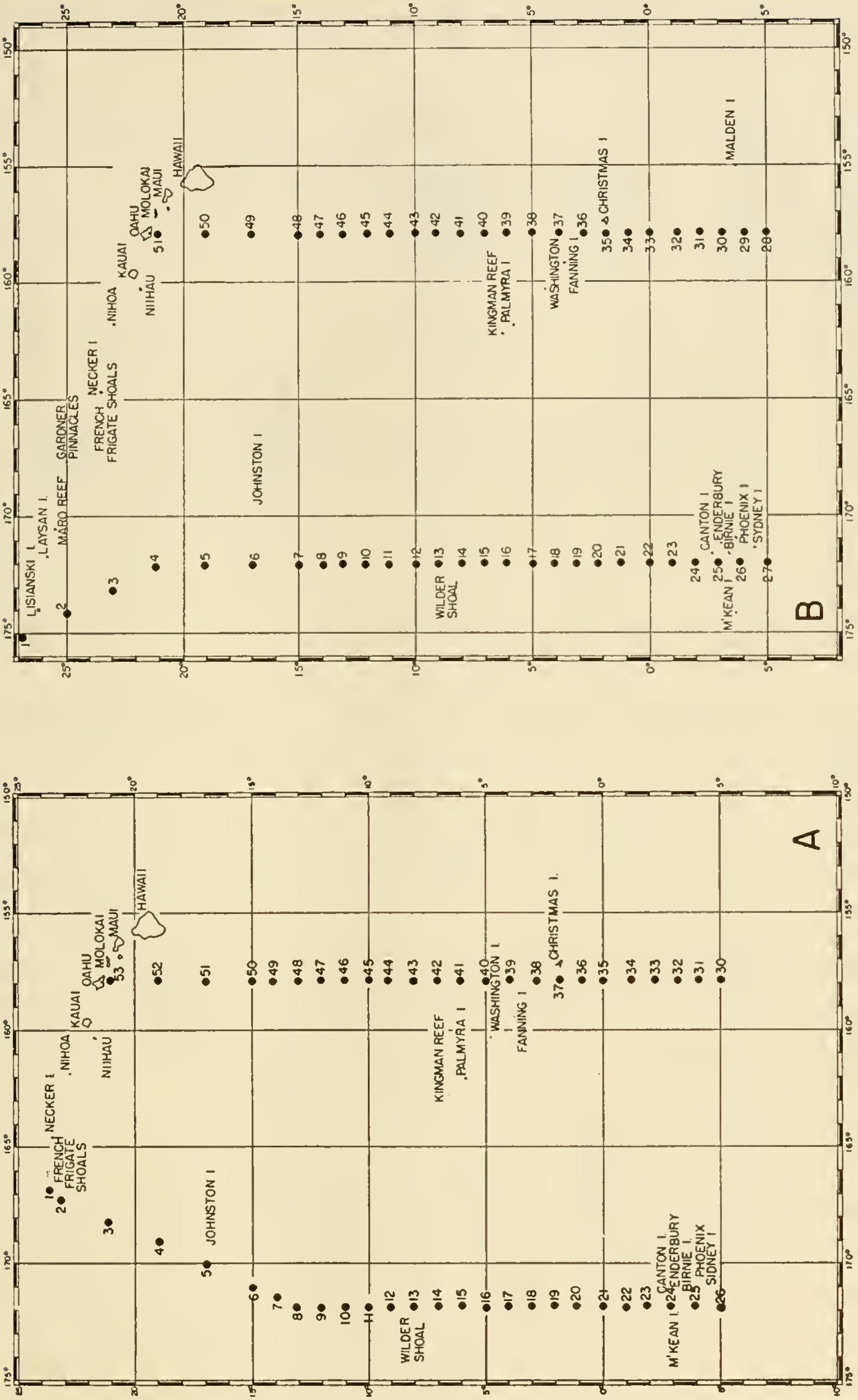

FIGURE 1a.—Plankton-station positions of the *Hugh M. Smith*. A, cruise 2, January–March, 1950. B, cruise 5, June–August 1950.

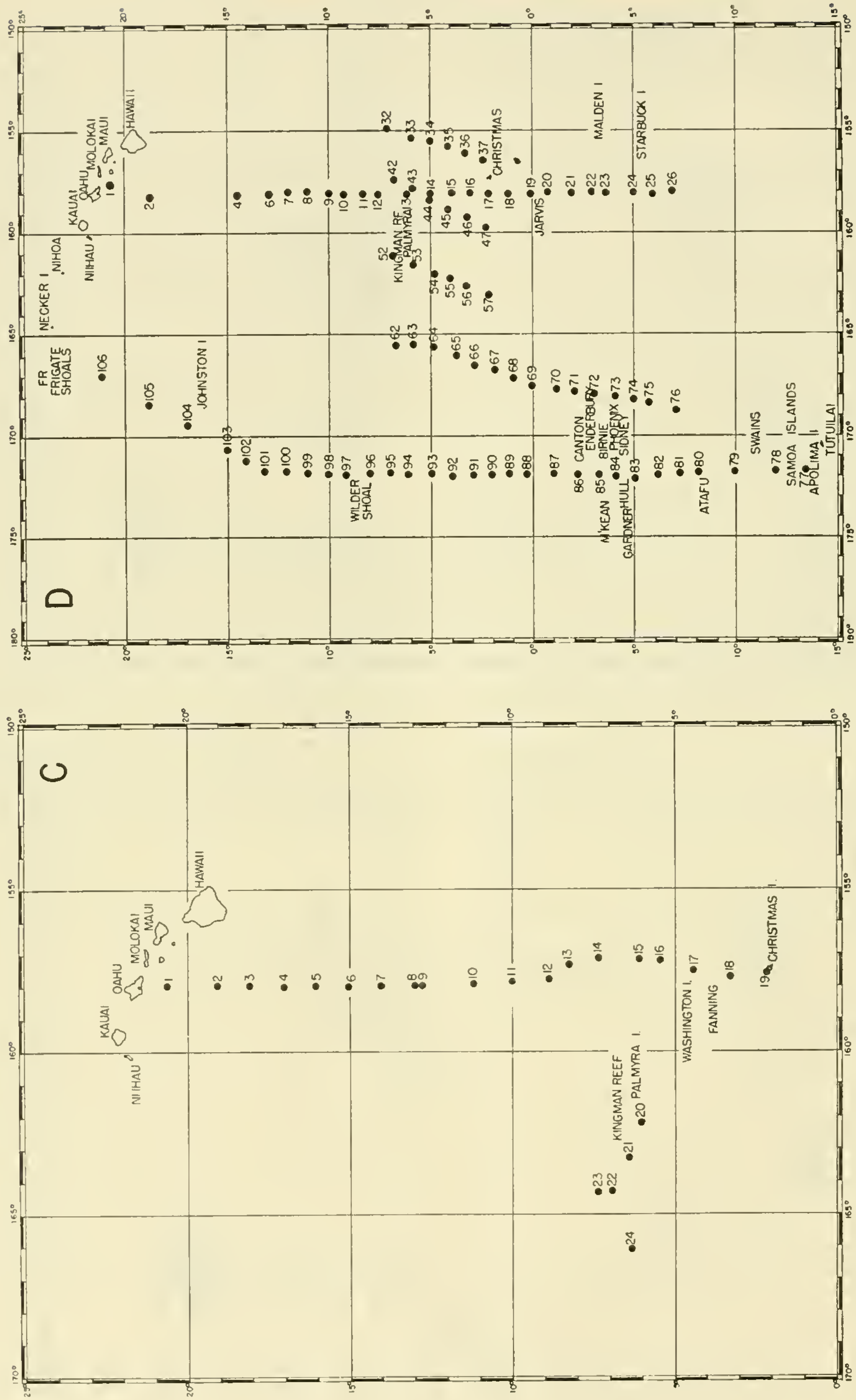

FIGURE 1b.—Plankton-station positions of the *Hugh M. Smith.* C, cruise 7, October–November, 1950. D, cruise 8, January–March, 1951.

TABLE 1.—*Cruise 2: Estimated numbers and volumes of zooplankton collected, January to March, 1950*

Station No.	Position		Date	Time [1]	Water strained, in m.^{3}	Number of organisms per m.^{3}	Wet volume, cc. per m.^{3}
	Latitude	Longitude					
A. Oblique tows to 200 m. (1-meter net, 30xxx mesh):							
1	23°54′ N.	166°51′ W.	Jan. 26	1100–1128	757.2	15	0.0079
3	20°59′ N.	168°16′ W.	Jan. 27	1401–1419	539.2	20	.0137
7	13°54′ N.	171°36′ W.	Jan. 30	0326–0351	937.5	15	.0115
9	12°02′ N.	172°04′ W.	do	2315–2337	837.5	15	.0129
11	10°02′ N.	171°55′ W.	Jan. 31	1946–2003	544.5	9	.0092
13	8°00′ N.	171°48′ W.	Feb. 1	1745–1805	631.2	25	.0177
16	6°07′ N.	171°56′ W.	Feb. 3	1300–1328	1,030.0	45	.0285
17	3°58′ N.	172°00′ W.	Feb. 4	0855–0921	837.5	43	.0349
19	2°00′ N.	172°05′ W.	Feb. 5	0245–0321	1,047.0	61	.0714
21	0°00	171°59′ W.	Feb. 6	0250–0326	1,104.0	109	.0826
23	2°00′ S.	172°02′ W.	do	2235–2257	782.5	25	.0549
25	4°00′ S.	171°58′ W.	Feb. 7	1646–1712	694.0	44	.0236
B. Oblique tows to 200 m. (2-meter net, 3⁄16-inch mesh, rear section 18xxx mesh):							
2	23°10′ N.	167°00′ W.	Jan. 26	1921–1959	6,766.0	1	.0003
6	15°00′ N.	171°06′ W.	Jan. 29	1746–1811	3,852.4	.8	.0019
8	13°00′ N.	172°00′ W.	Jan. 30	1213–1240	3,195.5	.3	.0009
10	11°03′ N.	172°00′ W.	Jan. 31	1035–1056	3,610.5	1	.0032
12	9°00′ N.	172°00′ W.	Feb. 1	0546–0635	8,951.4	7	.0040
14	7°00′ N.	172°00′ W.	Feb. 2	1827–1858	3,716.6	3	.0081
16	5°02′ N.	172°01′ W.	Feb. 4	0034–0112	5,232.2	3	.0101
18	2°56′ N.	172°04′ W.	do	1824–1855	4,644.9	10	.0117
20	1°01′ N.	172°09′ W.	Feb. 5	1624–1647	2,369.9	6	.0122
22	1°01′ S.	172°00′ W.	Feb. 6	1236–1259	2,453.4	5	.0114
24	3°00′ S.	172°04′ W.	Feb. 7	0755–0779	3,226.8	5	.0146
26	5°02′ S.	171°53′ W.	Feb. 8	0230–0252	2,579.6	1	.0012
C. Surface tows (1-meter net, 30xxx mesh):							
30	4°55′ S.	158°13′ W.	Feb. 18	0545–0616	1,300.5	83	.0451
32	3°06′ S.	158°21′ W.	Feb. 19	0212–0243	1,067.0	38	.0370
34	1°07′ S.	158°28′ W.	do	2200–2232	1,231.0	57	.0911
36	1°02′ N.	158°05′ W.	Feb. 20	1030–1101	1,357.2	64	.0721
38	3°02′ N.	157°51′ W.	Feb. 22	1820–1850	1,035.5	58	.0759
40	5°00′ N.	157°59′ W.	Feb. 23	1255–1326	1,139.0	26	.0088
42	7°00′ N.	157°58′ W.	Feb. 24	0725–0756	1,148.0	27	.0082
44	8°53′ N.	157°54′ W.	Feb. 25	0025–0056	1,112.0	62	.0622
46	11°02′ N.	158°06′ W.	do	2220–2302	1,284.8	19	.0139
48	13°02′ N.	157°51′ W.	Feb. 26	1830–1901	1,084.5	16	.0037
50	14°57′ N.	157°59′ W.	Feb. 27	1325–1356	1,332.5	5	.0022
52	19°00′ N.	157°42′ W.	Mar. 1	0215–0246	1,310.0	23	.0176
D. Surface tows (1-meter net, 18xxx mesh):							
31	3°53′ S.	157°47′ W.	Feb. 18	1604–1636	1,066.0	17	.0255
33	2°03′ S.	158°28′ W.	Feb. 19	1231–1304	1,105.5	3	.0054
35	0°04′ S.	158°22′ W.	Feb. 20	0900–0931	1,307.8	4	.0044
37	2°03′ N.	158°08′ W.	Feb. 21	2045–2116	1,272.5	18	.0520
39	4°03′ N.	157°53′ W.	Feb. 23	0412–0442	1,205.5	24	.0499
41	6°00′ N.	158°03′ W.	do	2150–2251	1,550.0	12	.0329
43	8°02′ N.	157°49′ W.	Feb. 24	1607–1638	1,190.5	6	.0049
45	9°55′ N.	157°54′ W.	Feb. 25	0952–1023	1,567.0	1	.0003
47	12°01′ N.	158°03′ W.	Feb. 26	0725–0755	1,772.8	1	.0003
49	14°00′ N.	157°51′ W.	Feb. 27	0427–0500	1,232.8	11	.0190
51	17°01′ N.	157°56′ W.	Feb. 28	0730–0801	1,620.0	2	.0019
53	20°54′ N.	158°04′ W.	Mar. 1	2056–2136	2,012.8	3	.0053

[1] Time corresponding to +11 zone time (Greenwich Civil Time −11 hours) was used for all stations 1 to 26, and +10 zone time on stations 30 to 53.

TABLE 2.—*Cruise 5: Estimated numbers and volumes of zooplankton collected, June to August, 1950*

[All tows oblique, surface to 200 m. to surface; all nets with body of 30xxx grit gauze, cod end of 56xxx grit gauze]

Station No.	Position		Date	Time [1]	Water strained in m.^{3}	Number of organisms per m.^{3}	Wet volume, cc. per m.^{3}
	Latitude	Longitude					
1	27°00′ N.	175°11′ W.	June 30	0945–1012	1,248.7	26	0.0118
2	25°00′ N.	174°10′ W.	July 1	0258–0325	1,322.7	46	.0271
3	22°58′ N.	173°00′ W.	do	2315–2337	1,343.9	40	.0175
4	21°00′ N.	172°00′ W.	July 2	0415–0431	739.5	33	.0254
5	19°00′ N.	171°52′ W.	July 3	0807–0831	1,254.8	35	.0174
6	17°01′ N.	171°46′ W.	do	1219–1246	1,434.4	22	.0388
7	15°00′ N.	171°54′ W.	July 4	1649–1710	888.1	45	.0216
8	14°00′ N.	171°57′ W.	July 5	0123–0145	854.8	40	.0234
9	13°00′ N.	172°01′ W.	do	0950–1019	1,327.5	32	.0125
10	12°00′ N.	172°00′ W.	do	1815–1833	882.8	14	.0084
11	11°03′ N.	172°00′ W.	July 6	0315–0342	1,333.3	34	.0374
12	9°54′ N.	172°02′ W.	do	1213–1244	1,777.0	20	.0252
13	8°54′ N.	172°00′ W.	do	2012–2036	1,190.2	31	.0301
14	7°59′ N.	171°57′ W.	July 7	0350–0420	1,623.7	18	.0203
15	6°59′ N.	171°46′ W.	do	1226–1258	1,579.4	27	.0204
16	6°02′ N.	171°56′ W.	do	2130–2201	1,382.2	30	.0338
17	5°00′ N.	172°02′ W.	July 8	0845–0918	1,821.1	40	.0226

Footnote at end of table.

TABLE 2.—*Cruise 5: Estimated numbers and volumes of zooplankton collected, June to August, 1950*—Con.

Station	Position		Date	Time [1]	Water strained, in m.^{3}	Number of organisms per m.^{3}	Wet volume, cc. per m.^{3}
	Latitude	Longitude					
18	4°00′ N.	172°03′ W.	...do.....	1659–1729	1,346.2	65	.0385
19	3°00′ N.	172°01′ W.	July 9	0036–0101	1,063.8	59	.0410
20	2°00′ N.	171°53′ W.	...do.....	0838–0909	1,809.2	58	.0330
21	0°54′ N.	172°12′ W.	...do.....	1746–1815	1,586.0	67	.0556
22	0°08′ S.	172°02′ W.	July 10	0143–0214	1,943.8	94	.0604
23	1°00′ S.	171°57′ W.	...do.....	0925–0951	1,256.9	107	.0742
24	2°00′ S.	171°55′ W.	...do.....	1740–1809	1,406.4	52	.0452
25	2°59′ S.	171°59′ W.	July 11	0133–0201	1,309.9	68	.0664
26	4°05′ S.	171°56′ W.	...do.....	1055–1127	1,585.3	36	.0230
27	5°04′ S.	171°58′ W.	...do.....	2110–2141	1,632.8	27	.0315
28	4°56′ S.	158°02′ W.	July 28	0556–0614	1,384.8	20	.0087
29	4°00′ S.	158°03′ W.	...do.....	1324–1338	642.8	47	.0239
30	3°03′ S.	158°00′ W.	...do.....	2137–2200	873.7	46	.0490
31	2°03′ S.	158°00′ W.	July 29	0550–0607	648.3	45	.0253
32	1°00′ S.	158°01′ W.	...do.....	1418–1436	996.0	43	.0239
33	0°02′ S.	157°58′ W.	...do.....	2221–2239	773.0	76	.0880
34	0°57′ N.	157°57′ W.	July 30	0646–0715	1,528.5	44	.0347
35	2°00′ N.	158°07′ W.	...do.....	1532–1553	851.2	62	.0658
36	3°00′ N.	157°58′ W.	...do.....	2302–2324	972.8	93	.0701
37	4°02′ N.	158°03′ W.	July 31	0640–0707	1,652.5	76	.0783
38	5°00′ N.	158°00′ W.	...do.....	1750–1816	1,175.4	74	.0691
39	6°00′ N.	157°57′ W.	Aug. 1	0144–0214	1,313.7	35	.0449
40	7°00′ N.	157°57′ W.	...do.....	0854–0919	954.3	43	.0258
41	8°00′ N.	157°50′ W.	...do.....	1620–1704	3,361.5	31	.0230
42	9°00′ N.	157°55′ W.	Aug. 2	0020–0046	1,136.6	38	.0531
43	10°00′ N.	157°53′ W.	...do.....	0744–0812	1,597.8	25	.0225
44	11°00′ N.	157°55′ W.	...do.....	1546–1615	1,141.7	40	.0242
45	11°59′ N.	158°04′ W.	...do.....	2343–0008	1,034.5	32	.0327
46	13°00′ N.	157°58′ W.	Aug. 3	0800–0827	1,455.8	19	.0158
47	14°00′ N.	157°54′ W.	...do.....	1639–1709	1,305.7	18	.0201
48	14°58′ N.	157°55′ W.	Aug. 4	0253–0311	592.8	19	.0246
49	17°00′ N.	158°08′ W.	...do.....	1741–1805	934.8	38	.0214
50	19°02′ N.	157°59′ W.	Aug. 5	1006–1031	1,035.0	29	.0357
51	20°53′ N.	158°02′ W.	...do.....	2300–2324	852.2	37	.0289

[1] +11 zone time on stations 1 to 27, +10 zone time on stations 28 to 51.

TABLE 3.—*Cruise 7: Estimated numbers and volumes of zooplanton collected, October to November 1950*

[All tows oblique, surface to 200 m. to surface; all nets with body of 30xxx grit gauze, cod end of 56xxx grit gauze]

Station No.	Position		Date	Time [1]	Water strained, in m.^{3}	Number of organisms per m.^{3}	Wet volume, cc. per m.^{3}
	Latitude	Longitude					
1	20°30′ N.	158°00′ W.	Oct. 17	1925–1955	952.8	44	0.0353
2	19°10′ N.	158°02′ W.	Oct. 18	0532–0600	897.3	44	.1025
3	18°13′ N.	158°00′ W.	...do.....	1326–1355	1,112.5	30	.0288
4	17°10′ N.	158°00′ W.	...do.....	2159–2225	683.7	27	.0208
5	16°11′ N.	157°57′ W.	Oct. 19	0506–0530	699.0	21	.0269
6	15°02′ N.	157°58′ W.	...do.....	1250–1318	999.2	14	.0300
7	14°03′ N.	157°59′ W.	...do.....	1921–1955	1,220.6	27	.0274
8	12°57′ N.	157°57′ W.	Oct. 20	0330–0353	730.6	64	.0567
9	12°25′ N.	158°00′ W.	...do.....	1729–1804	1,217.9	38	.0345
10	11°08′ N.	158°01′ W.	Oct. 21	1526–1556	1,373.5	42	.0296
11	10°01′ N.	157°55′ W.	Oct. 22	0724–0804	1,426.0	40	.0296
12	8°52′ N.	157°45′ W.	Oct. 23	0722–0751	956.9	37	.0169
13	8°05′ N.	157°15′ W.	Oct. 24	0742–0813	1,413.5	19	.0119
14	7°17′ N.	157°04′ W.	Oct. 25	0727–0805	1,698.8	32	.0182
15	5°57′ N.	157°05′ W.	Oct. 26	0737–0810	1,572.1	59	.0682
16	5°19′ N.	157°20′ W.	Oct. 27	0725–0809	2,206.2	65	.0566
17	4°23′ N.	157°30′ W.	Oct. 28	0912–0945	1,872.1	40	.0348
18	3°17′ N.	157°53′ W.	Oct. 29	0802–0837	1,314.0	50	.0653
19	2°01′ N.	157°34′ W.	Nov. 1	0812–0844	1,587.3	75	.0741
20	6°07′ N.	162°06′ W.	Nov. 6	0950–1028	1,930.3	28	.0204
21	6°13′ N.	163°05′ W.	Nov. 7	0810–0837	1,565.8	63	.0483
22	6°59′ N.	163°54′ W.	Nov. 8	0808–0841	1,749.1	22	.0149
23	7°24′ N.	164°25′ W.	Nov. 9	0806–0838	1,442.4	27	.0147
24	6°31′ N.	165°45′ W.	Nov. 10	0813–0847	1,521.5	23	.0166

+10 zone time on stations 1 to 21, +11 zone time on stations 22 to 24.

TABLE 4.—*Cruise 8: Estimated numbers and volumes of zooplankton collected, January to March, 1951*

[All tows oblique, surface to 200 m. to surface; all nets with body of 30xxx grit gauze, cod end of 56xxx grit gauze]

Station No.	Position		Date	Time [1]	Water strained, in m.^{3}	Number of organisms per m.^{3}	Wet volume, cc. per m.^{3}
	Latitude	Longitude					
1	20°48′ N.	157°30′ W.	Jan. 14	2012–2048	937.3	27	0.0154
2	18°47′ N.	158°01′ W.	Jan. 15	1449–1504	625.9	23	.0105
4	14°30′ N.	158°00′ W.	Jan. 17	0925–0940	433.1	43	.0236
6	12°57′ N.	157°58′ W.	do	2251–2318	819.0	46	.0310
7	11°59′ N.	157°50′ W.	Jan. 18	0811–0836	1,363.0	24	.0094
8	11°00′ N.	157°53′ W.	do	1633–1658	1,399.9	36	.0093
9	10°00′ N.	157°56′ W.	Jan. 19	0224–0255	1,830.5	30	.0251
10	9°00′ N.	157°58′ W.	do	1154–1216	985.1	33	.0166
11	8°04′ N.	157°58′ W.	do	2024–2047	1,244.0	31	.0190
12	7°08′ N.	157°58′ W.	Jan. 20	0615–0645	1,299.2	74	.0477
13	5°59′ N.	158°00′ W.	do	1505–1537	1,807.5	34	.0186
14	5°00′ N.	158°00′ W.	do	2338–2357	975.3	32	.0174
15	3°55′ N.	157°54′ W.	Jan. 21	1100–1118	984.1	31	.0118
16	3°02′ N.	157°57′ W.	do	2135–2155	1,018.2	43	.0255
17	2°00′ N.	158°01′ W.	Jan. 22	0802–0831	1,625.2	30	.0146
18	0°58′ N.	158°07′ W.	do	1730–1754	1,529.1	33	.0220
19	0°01′ N.	158°02′ W.	Jan. 23	0323–0356	1,925.6	32	.0370
20	0°55′ S.	157°54′ W.	do	1208–1233	1,509.4	90	.0478
21	2°00′ S.	158°00′ W.	do	2312–2336	1,273.4	80	.0558
22	3°04′ S.	158°05′ W.	Jan. 24	0744–0808	1,270.9	48	.0257
23	4°00′ S.	158°00′ W.	do	1550–1614	1,070.4	36	.0178
24	5°00′ S.	158°00′ W.	do	2330–2350	885.8	46	.0666
25	6°01′ S.	158°06′ W.	Jan. 25	0741–0806	1,234.2	48	.0266
26	7°00′ S.	158°01′ W.	do	1548–1616	1,352.6	23	.0092
32	6°57′ N.	154°56′ W.	Jan. 31	0208–0238	1,521.4	39	.0251
33	5°58′ N.	155°08′ W.	do	1040–1060	948.4	35	.0325
34	5°00′ N.	155°28′ W.	do	1836–1902	1,483.2	35	.0284
35	4°04′ N.	155°46′ W.	Feb. 1	0223–0250	1,254.0	49	.0340
36	3°06′ N.	156°09′ W.	do	1040–1061	1,676.0	66	.0348
37	2°00′ N.	156°30′ W.	do	1835–1902	1,556.8	46	.0316
42	6°50′ N.	157°33′ W.	Feb. 3	0612–0639	1,680.3	22	.0145
43	6°04′ N.	157°53′ W.	do	1337–1404	1,401.1	21	.0126
44	5°00′ N.	158°34′ W.	do	2245–2309	1,245.7	31	.0204
45	4°05′ N.	158°53′ W.	Feb. 4	0706–0727	1,063.9	41	.0177
46	3°03′ N.	159°10′ W.	Feb. 6	0441–0513	1,881.2	21	.0254
47	1°57′ N.	159°39′ W.	do	1343–1419	1,619.8	26	.0106
52	6°59′ N.	161°12′ W.	Feb. 7	1025–1049	1,744.5	29	.0224
53	5°55′ N.	161°28′ W.	Feb. 8	2030–2056	1,914.2	33	.0313
54	4°52′ N.	161°48′ W.	Feb. 9	0443–0513	1,835.9	33	.0276
55	3°58′ N.	162°02′ W.	do	1119–1143	1,488.0	17	.0118
56	2°58′ N.	162°25′ W.	do	1919–1946	1,819 0	30	.0303
57	2°00′ N.	162°57′ W.	Feb. 10	0259–0327	1,514.6	31	.0354
62	6°44′ N.	165°23′ W.	Feb. 11	1652–1718	1,330.2	21	.0170
63	5°51′ N.	165°28′ W.	Feb. 12	0021–0048	1,647.2	31	.0368
64	4°58′ N.	165°35′ W.	do	0758–0824	1,432.3	23	.0176
65	3°59′ N.	166°01′ W.	do	1626–1653	1,743.6	22	.0118
66	3°00′ N.	166°36′ W.	Feb. 13	0100–0130	1,760.7	37	.0359
67	2°04′ N.	166°47′ W.	do	0848–0913	1,618.2	26	.0248
68	1°02′ N.	167°02′ W.	do	1815–1839	1,116.2	52	.0408
69	0°01′ N.	167°23′ W.	Feb. 14	0240–0308	1,433.5	47	.0473
70	1°05′ S.	167°36′ W.	do	1132–1156	1,420.4	23	.0172
71	2°01′ S.	167°42′ W.	do	1903–1930	1,785.5	37	.0320
72	3°05′ S.	167°50′ W.	Feb. 15	0323–0353	1,740.7	34	.0295
73	4°00′ S.	167°58′ W.	do	1041–1109	2,008.7	20	.0175
74	5°03′ S.	168°09′ W.	do	1819–1848	1,942.1	19	.0175
75	5°59′ S.	168°29′ W.	Feb. 16	0208–0241	2,424.3	33	.0332
76	7°04′ S.	168°48′ W.	do	0923–0953	2,308.6	24	.0100
77	14°30′ S.	171°51′ W.	Feb. 26	1931–1958	1,876.1	28	.0154
78	11°56′ S.	171°59′ W.	Feb. 27	1129–1157	1,918 4	26	.0115
79	10°05′ S.	171°52′ W.	Feb. 28	0245–0309	1,735.6	41	.0226
80	8°00′ S.	171°56′ W.	do	1821–1846	1,452.5	29	.0153
81	7°01′ S.	171°54′ W.	Mar. 1	0238–0303	1,045.2	52	.0291
82	5°59′ S.	172°00′ W.	do	1118–1144	1,399.9	22	.0100
83	5°00′ S.	172°15′ W.	do	1930–1955	1,507.6	22	.0202
84	4°00′ S.	172°06′ W.	Mar. 2	0735–0758	1,510.7	18	.0101
85	3°00′ S.	171°50′ W.	do	1537–1605	1,510.7	20	.0146
86	2°00′ S.	172°02′ W.	Mar. 3	1612–1641	1,593.0	21	.0109
87	0°57′ S.	172°00′ W.	Mar. 4	0047–0115	1,392.3	43	.0394
88	0°09′ N.	171°58′ W.	do	0926–0947	1,066.0	56	.0345
89	1°04′ N.	172°00′ W.	dn	1702–1727	979.6	73	.0308
90	1°54′ N.	172°02′ W.	Mar. 5	0034–0101	1,854.7	57	.0548
91	2°48′ N.	172°04′ W.	do	0834–0858	1,332.4	48	.0435
92	3°57′ N.	172°02′ W.	do	1816–1842	1,221.9	44	.0367
93	4°56′ N.	171°54′ W.	Mar. 6	0249–0315	1,621.0	51	.0369
94	5°55′ N.	171°50′ W.	do	1105–1130	1,428.2	43	.0242
95	6°58′ N.	171°49′ W.	do	1939–2011	1,907.6	24	.0244
96	7°56′ N.	171°51′ W.	Mar. 7	0407–0433	1,498.1	22	.0139
97	9°00′ N.	171°58′ W.	do	1315–1339	1,639.7	13	.0094
98	10°02′ N.	171°56′ W.	do	2147–2213	1,538.1	22	.0127
99	11°02′ N.	171°52′ W.	Mar. 8	0602–0629	1,576.9	23	.0115
100	12°00′ N.	171°52′ W.	do	1417–1443	1,507.0	11	.0097
101	13°01′ N.	171°48′ W.	do	2236–2301	1,720.5	20	.0192
102	13°58′ N.	171°24′ W.	Mar. 9	0650–0713	1,274.5	15	.0096
103	15°00′ N.	170°52′ W.	do	1557–1619	1,313.9	23	.0100
104	16°58′ N.	169°42′ W.	Mar. 10	0913–0940	1,993.3	25	.0181
105	18°58′ N.	168°27′ W.	Mar. 11	0207–0235	1,941.0	17	.0145
106	20°59′ N.	167°07′ W.	do	1913–1940	1,938.5	24	.0145

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[1] +10 zone time on stations 1 to 49, +11 zone time on stations 50 to 106.

Cruises 2, 5, and 8 were combined hydrographic and plankton cruises, and thus provide information on currents, temperatures, oxygen, and inorganic phosphate for comparison with the zooplankton abundance. On cruise 7, which was a combination longline-fishing and plankton cruise, subsurface (to approximately 800 feet) and surface temperatures were obtained at all plankton stations.

SAMPLING IN THE FIELD

Although the primary aim of our plankton sampling was to obtain information on the zooplankton populations of different ocean areas, a secondary objective was to collect tuna eggs and larvae for use in the study of the spawning habits of tuna. Sampling methods and procedures were therefore designed to contribute information toward both objectives.

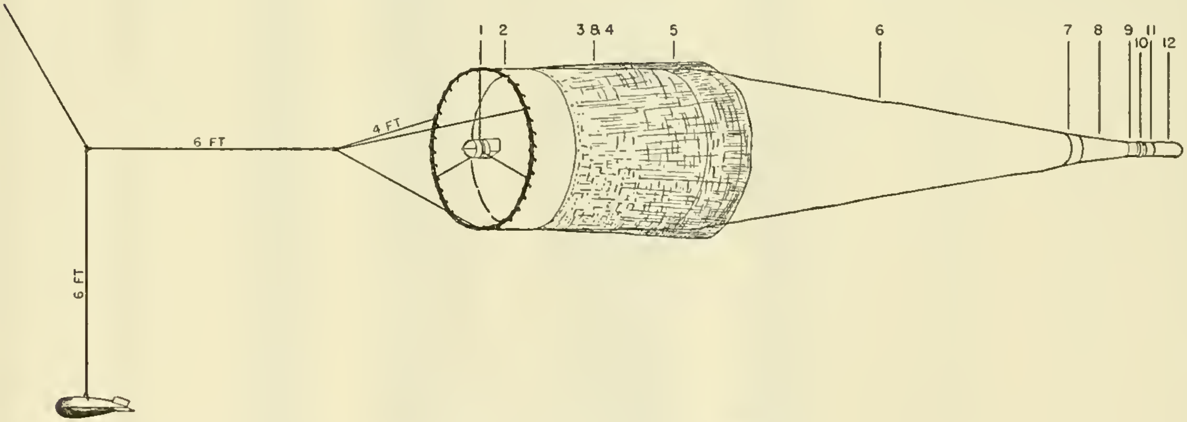
Plankton nets of the following three types were used on cruise 2:

1. 1-meter (mouth diameter) net with body (front and middle sections) of 30xxx silk grit gauze (width of apertures 0.65 mm.), rear section and bag of 56xxx silk grit gauze (width of apertures 0.31 mm.) ;
2. 1-meter net with body of 18xxx grit gauze (width of apertures 1.3 mm.), rear section and bag of 30xxx grit gauze; and
3. 2-meter net with body of $3/16$ inch square cotton mesh, rear section and bag of 18xxx grit gauze.

The results of this cruise showed that the 1-meter net with a body of 18xxx grit gauze retained considerably less zooplankton than the 30xxx net; the 2-meter net captured almost no zooplankton and few fish or other large forms. Some preliminary tows, the results of which are not included in this report, indicated that nets of 56xxx and 72xxx grit gauze retained the larger phytoplankton as well as zooplankton, thus making analysis of the sample more difficult. On the basis of this experimentation and a review of methods used by other investigators for sampling zooplankton, we adopted the 1-meter, 30xxx net (fig. 2) as being the best suited for our purposes. Nets of this type were employed exclusively on cruises 5, 7, and 8.

In this study, sampling was limited to a single tow at each station. For this reason, we chose to use, for the greater part, an oblique tow (surface to 200 meters to surface) of approximately 30 minutes' duration. On cruise 2, both oblique and surface tows were used, but on all subsequent cruises the oblique tow was the only type employed.

The merits of the oblique haul have been well demonstrated by Winsor and Clark (1940). They obtained a percentage standard deviation (coefficient of variation) for a single observation of 31 percent for oblique hauls, 53 percent for verti-



DESCRIPTION OF PLANKTON NET SECTIONS

	1	2	3	4	5	6	7	8	9	10	11	12
MATERIAL	GALV IRON RING	12 OZ. CANVAS	30 XXX GRIT GAUGE	3/16" BAIT NETTING	10 OZ. CANVAS	30 XXX GRIT GAUGE	10 OZ. CANVAS	56 XXX GRIT GAUGE	10 OZ CANVAS	BUCKET COUPLING	10 OZ. CANVAS	56 XXX GRIT GAUGE
DIAMETER	39.4"	39.4"	39.4"	40"	39.4"	39.4" - 8"	8"	8"-4"	4"	4"	4"	4"
LENGTH	7/8" THICK	12"	38"	48"	10"	110"	3"	18"	2 1/2"	2 1/2"	2 1/2"	9"

FIGURE 2.—Diagram and description of the 1-meter net used in this investigation, showing general construction of the net and method of attachment to the weight and towing lines.

cal hauls, and 124 percent for horizontal hauls; and they concluded that oblique hauls gave more reliable and consistent results than vertical or horizontal hauls. The more erratic nature of the surface haul, as compared with the oblique, is evident from figure 4, showing the results of cruise 2, on which both types of haul were used.

That the oblique and surface hauls made on this cruise were not greatly different, however, is indicated by a comparison of the volumes (cc./m.^{3}) obtained at 12 pairs of stations (table 1, A and C), the members of each pair occurring at approximately the same latitude, but at a different longitude (fig. 1, A). It may be shown that the mean difference (0.00575 cc./m.^{3}) between the paired hauls does not differ significantly from 0 ($P=0.4$). Therefore, the few surface hauls made on cruise 2 have been included in this report but have been omitted from the statistical analysis dealing with sources of variation and correlations with environmental factors.

On cruises 2, 5, and 8, stations were visited consecutively regardless of the time of day or night. Because of this practice, the effects of diurnal migration must be considered in an evaluation of zooplankton abundance at any place and time. Initially we had hoped, through the use of the oblique tow to 200 meters' depth, to nullify to a large extent differences in the samples caused by vertical movements of the plankton. That we did not succeed is indicated by close perusal of the tables of data, particularly for cruise 5 (table 2), and cruise 8 (table 4), comparing successive day and night hauls. It will be seen that usually the night hauls produced a higher volume than the day hauls. This tendency will be discussed later in the section on sources of variation in zooplankton volumes.

Another problem that adds to the difficulty of estimating zooplankton abundance is the uneven distribution of plankton organisms. This has been referred to by many planktologists and is emphasized by Haeckel (1890), Herdman (1923), Gardiner (1931), Hardy (1936), Wilson (1942), Riley and Bumpus (1946), Sears (1950), and others. By our method of straining a large volume of water, averaging over 1,000 cubic meters per haul, and of sampling in uniform fashion from the surface to 200 meters' depth, it is assumed that the variation in catch due to the uneven distribution of organisms is minimized.

The amount of water strained during each haul was measured by a flow meter suspended in the mouth of the net. Each flow meter was calibrated by towing it over a measured course at approximately the same speed used in making the plankton hauls. The flow meters were calibrated before and after each cruise, and the average of these calibrations was used to compute the volume of water strained in cubic meters for each haul during that cruise. Within a limited range of towing speeds the number of revolutions registered by the meter indicates the length of the water column passing through the net; multiplying this length by the area of the mouth of the net gives an estimate of the water volume strained.

There has never been evidence of clogging on any of the tows, possibly because of the relatively coarse mesh used in the nets and the general paucity of plankton.

In making the tow, the net and a 75-pound streamlined weight were attached to the cable, which was paid out slowly at uniform speed. As the net was lowered, the length of wire out and the angle of stray were recorded at 2-minute intervals. As soon as a calculated depth of 200 meters was reached, the net was retrieved at a slow, uniform speed. The wire angle and the length of wire out were again recorded at 2-minute intervals. At a towing speed of about 2 knots, an oblique tow to a depth of 200 meters and return required about 30 minutes. A graph of depth reached plotted against time (fig. 3) for 3 tows made on cruise 5, shows that, for practical purposes, equal amounts of time are spent at all depths; i. e., assuming the towing wire represents a straight line in the water, the net strains approximately the same amount of water for each meter of depth passed through. It is recognized that the towing wire does not actually describe a straight line during the tow, but the error caused by a slight curve is small.

When the net reached the surface at the end of a tow, it was lifted out of the water, suspended vertically from a boom, and washed down with a hose. The plankton bucket was then detached, and its contents were washed into an enameled pan. Next, the sample was transferred to a 1-quart fruit jar, and sufficient formalin was added to approximate a 10-percent solution. The formalin was neutralized with borax. A completed label was placed in the jar.

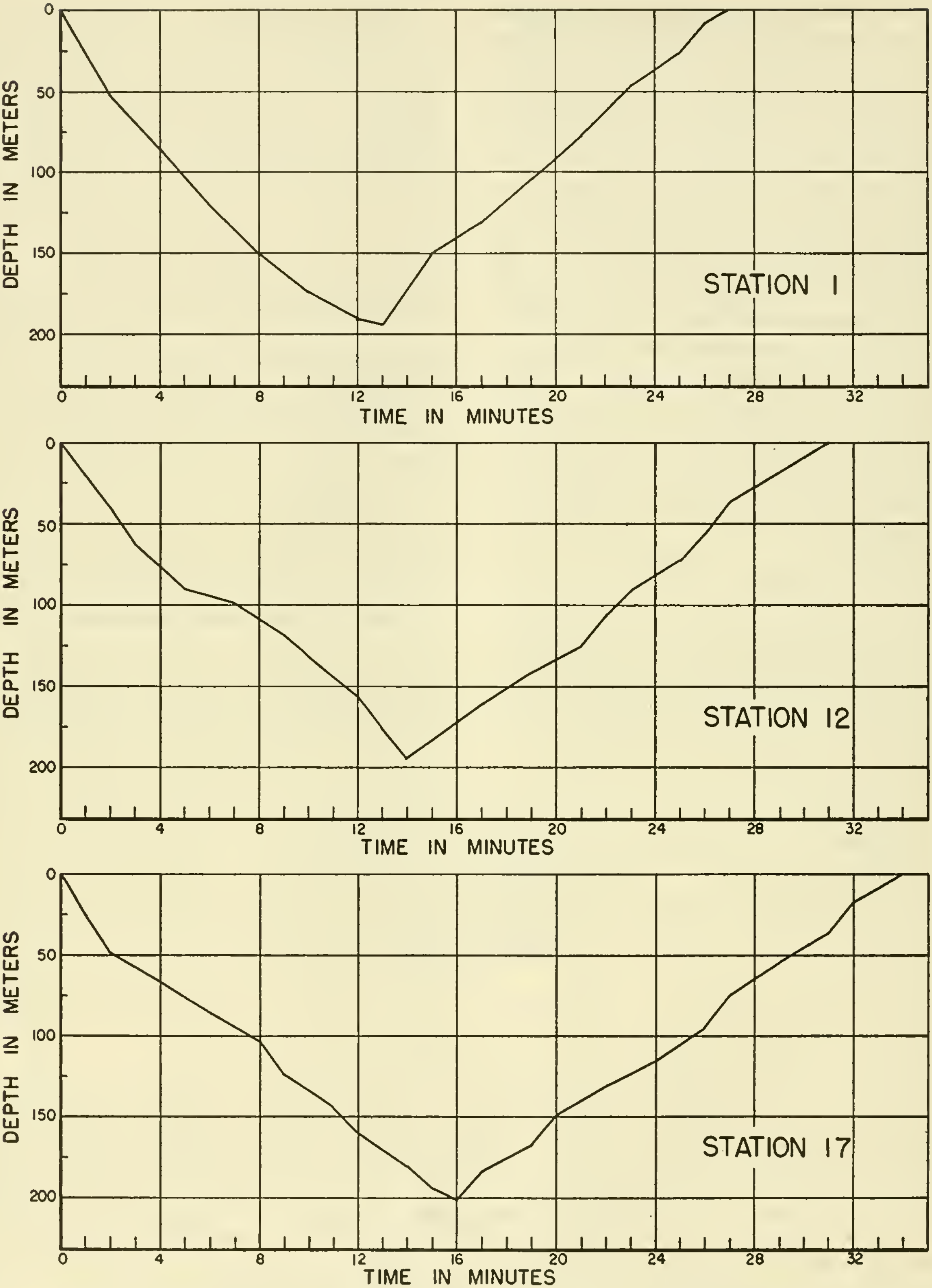


FIGURE 3.—Graphs of three typical tows (stations 1, 12, and 17) of cruise 5, showing depth estimated from wire angle and wire out.

TREATMENT OF SAMPLES

The zooplankton collections received the following treatment in the laboratory:

1. All fish eggs and larvae were removed. In all cases these have amounted to a negligible fraction of the sample and were omitted from the volume measurement.

2. Several portions of the remaining sample were examined microscopically, and the various groups of organisms were identified at least to the order. Where possible without great expenditure of time and effort, identifications were made to the genus and species. A list of constituents was thus compiled for each sample.

3. All organisms whose longest dimension was greater than 5 centimeters were removed from the sample. Such organisms occurred infrequently and were not considered in the analysis.

4. By means of a splitting chamber the remaining sample was then divided into halves; one-half was labeled and placed in a reference collection, the other was used for the organism counts and displacement-volume determinations.

5. In making the count, a given portion (usually a fourth, occasionally a half or an eighth) of the half reserved for this purpose, was placed in a 15 by 20 cm. counting chamber, thoroughly mixed, and distributed as evenly as possible over the entire cell area. Organisms between 2 and 5 cm. in their longest dimension were enumerated in counting-chamber fields 5 cm. square, without magnification. For counting smaller organisms (0.5 millimeter to 2.0 cm. in longest dimension), the counting cell was placed over a Wolffhuegel plate under a binocular microscope. Organisms in this size category were counted in fields 1 cm. square on the Wolffhuegel plate. Organisms less than 0.5 mm. long were identified but not counted, since the mesh of the nets employed was not sufficiently fine to catch these forms quantitatively. In counting organisms of all sizes, either (a) enough fields were counted to yield a minimum count of 100 for each type of organism, or (b) 10 fields were counted, whichever was reached first. The estimated number of zooplankters of each species or category in the total sample (minus fish eggs and larvae and organisms larger than 5 cm.) was computed by use of the following formula:

$$E=\frac{C\cdot A}{f\cdot a\cdot n}$$

where

E=estimated number in total sample
C=counted number
A=area of cell
f=fraction of total sample in the counting cell
a=area of field
n=number of fields counted

The estimated total number of zooplankters in the sample equals the sum of E values, i. e., the sum of the estimated numbers for each type or group of organisms. The estimated number per cubic meter of water was obtained by dividing the estimated total number in the sample by the cubic meters of water strained.

6. To measure the displacement volume, the half of the sample used for the organism counts was poured into a draining sock of 56xxx grit gauze to filter off the preserving liquid. The drained plankton was then placed in a 50- or 100-milliliter graduated cylinder, depending upon the size of the sample. By means of a burette a known volume of water was added to the drained plankton. The difference between the volume of the plankton plus the added liquid and the volume of liquid alone is the displacement volume or "wet volume" of the plankton half-sample. This figure was doubled to obtain the computed volume of the entire original sample (minus fish eggs and larvae and organisms larger than 5 cm.). When divided by cubic meters of water strained, this gave the volume (in cubic centimeters) of zooplankton per cubic meter of water.

The plankton counts given in this report, therefore, include those organisms between 0.5 mm. and 5 cm., longest dimensions; the volume measurements include all organisms in the sample less than 5 cm. in length.

Almost all stations occupied on the four cruises were in areas where the depth of water is 2,000 to 3,000 fathoms (roughly 4,000 to 6,000 meters). By sampling to a calculated depth of 200 meters (the actual depth attained was probably within 10 percent of this) we have done little more than "scratch the surface." No information was obtained on plankton abundance and distribution below the sampled depth. Therefore, we believe that our results are most properly expressed in terms of organisms per cubic meter in the upper 200 meters of water. If an estimate is desired of the areal abundance, i. e., the quantity of zooplankton in a column of water 200 meters in height and 1 meter square in cross section, it may be obtained by multiplying by 200 the numbers and volumes of zooplankton per cubic meter given in tables 1, 2, 3, and 4.

COMPOSITION OF THE ZOOPLANKTON

Tables 5, 6, 7, and 8 show for each cruise and station the percentage composition by number of the 6 major constituents of the zooplankton. It is evident that copepods—by number—were consistently the most important constituent. The chaetognaths usually were second in rank, followed by the tunicates, euphausiids, siphonophores, and foraminifers. At several stations other groups, such as radiolarians, annelids, amphipods, ostracods, and pteropods occurred in considerable numbers, but on the average these animals formed a very small percentage of the collections. As might be expected, the results vary to some extent from station to station; but when the data are summarized, as in table 9, there is revealed a marked and surprising uniformity in composition for the different longitudes and cruises. The percentages given are computed from the sums of estimated numbers for all stations. Percentages by volume for the separate groups were not determined.

The 210 samples include only a few instances of swarming: Collections taken at stations 7 and 9, cruise 5, contained unusually high percentages (60 and 58 percent) of foraminifers; the collection made at station 2, cruise 7, contained a high and unusual percentage (51 percent) of hyperid amphipods. In each case there was no marked change in number for the other major constituents.

As all of our plankton stations were located in the open ocean with very few within 100 miles of land, the collections consisted primarily of such forms as are permanently planktonic throughout their lives (holoplankton), and contained very few transitory young and larval stages (meroplankton) of bottom-dwelling forms such as echinoderms, crabs, and clams.

TABLE 5.—*Cruise 2: Percentage, by number, of six major constituents of zooplankton collections*

[Values less than 1 percent omitted]

Station No.	Copepoda	Chaetognatha	Tunicata	Euphausiacea	Siphonophora	Foraminifera	Miscellaneous
A. Oblique tows to 200 m. (1-meter net, 30xxx mesh):							
1	47	17	13	1	4	-------	17
3	35	19	31	4	2	1	8
7	64	10	1	6	2	-------	17
9	65	14	4	6	2	-------	9
11	50	16	11	4	3	1	15
13	61	10	3	4	-------	8	13
15	62	15	3	6	8	5	1
17	61	10	6	3	4	11	5
19	55	19	11	4	2	3	6
21	62	22	3	4	-------	1	7
23	66	16	2	7	2	-------	7
25	68	16	3	2	4	3	4
B. Oblique tows to 200 m. (2-meter net, 3/16-inch mesh, rear section 18xxx mesh):							
2	62	4	14	2	2	-------	16
6	34	-------	6	6	22	-------	32
8	56	6	8	6	8	-------	16
10	20	38	20	-------	17	1	4
12	47	16	11	6	10	-------	10
14	44	13	9	4	9	1	20
16	36	15	8	13	10	-------	18
18	67	12	3	4	5	-------	9
20	62	17	9	4	2	-------	6
22	67	20	------	3	5	-------	4
24	51	19	------	3	19	-------	7
26	19	21	4	12	8	-------	36
C. Surface tows (1-meter net, 30xxx mesh):							
30	79	11	3	3	-------	-------	3
32	65	12	9	6	3	-------	4
34	53	10	10	14	2	1	10
36	54	21	6	10	-------	6	2
38	43	15	15	10	1	4	12
40	51	26	16	-------	2	2	3
42	51	9	24	2	5	3	6
44	70	5	7	6	3	1	8
46	76	8	2	5	2	5	2
48	68	10	2	2	1	9	8
50	47	19	21	1	3	6	3
52	50	10	12	2	4	1	21
D. Surface tows (1-meter net, 18xxx mesh):							
31	50	14	------	26	3	-------	7
33	33	43	12	2	8	-------	2
35	24	37	18	-------	10	-------	11
37	33	18	9	22	9	-------	9
39	28	29	2	25	9	-------	7
41	57	6	5	25	4	-------	3
43	47	28	8	-------	6	-------	9
45	29	5	8	-------	12	-------	46
47	47	6	8	-------	24	-------	15
49	52	12	2	29	3	2	0
51	16	25	7	-------	13	1	38
53	37	11	8	-------	12	-------	32

TABLE 6.—*Cruise 5: Percentage, by number, of six major constituents of zooplankton collections*

[Values less than 1 percent omitted]

Station No.	Copepoda	Chaetognatha	Tunicata	Euphausiacea	Siphonophora	Foraminifera	Miscellaneous
1	53	4	9	4	-------	10	19
2	44	4	6	9	-------	6	30
3	58	6	8	5	3	2	18
4	35	7	11	1	2	21	23
5	46	5	8	6	3	12	20
6	41	7	3	12	5	20	12
7	25	4	4	-------	2	60	4
8	52	1	2	-------	3	34	7
9	22	6	3	2	1	58	8
10	66	11	6	2	-------	9	6
11	62	12	2	4	4	7	9

TABLE 6.—*Cruise 5: Percentage, by number, of six major constituents of zooplankton collections*—Continued

Station No.	Copepoda	Chaetognatha	Tunicata	Euphausiacea	Siphonophora	Foraminifera	Miscellaneous
12	73	8	3	1	8	--------	6
13	61	14	6	4	1	2	12
14	77	3	3	3	3	--------	11
15	59	9	5	2	7	11	7
16	52	6	5	2	8	3	24
17	67	5	3	4	4	2	15
18	55	11	8	3	10	2	11
19	68	4	8	8	5	2	5
20	60	9	8	6	4	2	11
21	61	11	6	6	1	--------	14
22	56	8	5	6	10	5	10
23	60	8	5	4	7	7	9
24	57	10	3	8	4	1	17
25	54	12	9	5	7	2	11
26	67	13	7	2	4	--------	7
27	61	16	4	8	2	--------	8
28	70	9	7	4	2	--------	8
29	51	10	5	4	--------	9	20
30	47	10	7	3	2	6	25
31	56	9	4	7	2	8	14
32	56	12	8	4	1	3	16
33	55	14	4	6	3	4	14
34	53	17	4	2	2	9	13
35	35	16	3	3	4	26	13
36	39	9	7	3	5	12	25
37	50	8	7	4	4	11	16
38	52	5	6	3	4	13	17
39	41	5	8	6	4	19	17
40	56	14	4	2	2	9	13
41	60	6	1	1	5	10	8
42	49	11	4	6	2	11	17
43	58	18	4	2	3	4	11
44	53	15	6	3	4	8	11
45	61	13	2	2	3	11	8
46	63	9	9	6	2	3	8
47	65	11	4	2	3	11	4
48	35	6	31	1	--------	21	6
49	58	2	5	1	4	10	20
50	58	8	6	5	3	2	18
51	51	4	10	5	5	3	22

TABLE 7.—*Cruise 7: Percentage, by number, of six major constituents of zooplankton collections*

[Values less than 1 percent omitted]

Station No.	Copepoda	Chaetognatha	Tunicata	Euphausiacea	Siphonophora	Foraminifera	Miscellaneous
1	47	6	4	4	5	7	27
2	24	5	2	5	2	2	60
3	51	13	4		8	6	14
4	51	12	16	4	1	6	10
5	57	7	10	3	5	7	11
6	59	21	4	2	--------	11	3
7	56	12	3	4	4	6	15
8	68	11	5	5	4	2	5
9	68	9	5	2	2	2	12
10	78	6	4	--------	1	2	8
11	60	8	14	--------	3	2	12
12	75	6	6	3	4	1	5
13	63	8	6	2	10	3	8
14	78	4	3	2	2	2	9
15	52	24	4	4	3	2	11
16	63	11	2	2	4	5	13
17	55	17	4	4	4	6	10
18	61	12	4	2	7	3	11
19	60	16	2	1	5	2	14
20	64	14	2	3	7	--------	10
21	60	12	7	4	6	1	10
22	66	8	2	3	6	--------	15
23	62	14	5	5	3	1	10
24	62	6	11	5	4	2	10

TABLE 8.—*Cruise 8: Percentage, by number, of six major constituents of zooplankton collections*

[Values less than 1 percent omitted]

Station No.	Copepoda	Chaetognatha	Tunicata	Euphausiacea	Siphonophora	Foraminifera	Miscellaneous
1	36	10	11	9	6	--------	27
2	52	11	10	3	8	--------	16
4	49	10	12	2	10	13	4
6	70	6	4	4	1	7	8
7	58	11	2	3	3	11	12
8	64	9	3	2	6	8	8
9	60	4	19	3	3	4	7
10	66	4	6	3	9	6	6
11	58	4	4	6	2	12	14
12	63	5	1	10	4	4	13
13	59	10	4	7	4	3	13
14	56	16	2	11	2	2	11
15	61	14	2	7	1	2	13
16	58	12	4	4	7	4	11
17	49	16	3	5	6	7	14
18	65	10	6	6	3	--------	10
19	58	11	4	8	3	2	14
20	54	14	4	3	6	9	10
21	52	16	2	13	4	3	10
22	59	20	9	3	--------	3	6
23	63	21	3	3	--------	3	6
24	51	17	2	11	3	6	10
25	59	17	12	4	2	4	2
26	66	20	8	--------	3	--------	3
32	64	8	4	8	4	--------	12
33	56	22	8	3	4	--------	7
34	64	14	4	6	5	--------	7
35	55	16	6	7	6	--------	9
36	57	19	4	3	4	2	11
37	50	22	2	10	5	1	10
42	68	8	--------	11	3	--------	10
43	74	11	2	4	1	--------	8
44	66	12	3	8	1	--------	10
45	56	19	4	9	2	--------	10
46	59	22	--------	10	4	--------	4
47	59	10	10	5	2	--------	13
52	62	17	7	1	4	3	6
53	62	12	5	6	3	2	10
54	55	17	6	6	2	--------	13
55	54	22	7	2	1	4	10
56	51	13	8	2	3	--------	22
57	56	20	2	11	2	1	8
62	64	13	3	2	4	2	12
63	58	14	5	9	3	3	8
64	59	12	3	9	4	4	9
65	63	21	6	2	1	--------	6
66	61	6	7	7	5	4	10
67	56	19	5	2	2	2	14
68	47	18	2	2	4	7	20
69	67	8	3	6	3	3	10
70	62	18	4	1	4	2	9
71	53	10	4	7	8	3	15
72	55	11	2	6	9	2	15
73	60	22	8	2	1	2	5
74	55	24	10	6	2	--------	3
75	67	11	1	8	2	--------	10
76	51	24	9	5	3	--------	8
77	43	6	5	9	14	1	22
78	55	7	6	1	11	4	16
79	66	12	5	3	7	1	6
80	74	7	3	2	3	--------	10
81	65	16	5	5	3	--------	6
82	74	10	5	3	2	--------	6
83	59	19	--------	9	2	--------	11
84	68	10	6	1	2	2	11
85	51	19	12	2	10	--------	5
86	55	27	4	6	--------	--------	8
87	54	19	5	6	5	1	10
88	51	17	5	4	6	1	16
89	49	17	7	3	4	5	15
90	60	10	5	6	3	3	13
91	46	15	10	3	5	2	19
92	47	17	4	7	9	2	14
93	70	10	1	5	4	--------	9
94	56	18	7	4	5	4	6
95	72	6	3	4	3	2	10
96	72	7	7	7	--------	--------	5
97	53	17	10	2	4	8	6
98	59	9	10	5	4	--------	12
99	55	13	6	5	4	4	13
100	43	8	16	1	9	2	21
101	57	9	11	4	8	--------	10
102	54	14	1	9	2	--------	19
103	67	2	9	3	6	--------	13
104	67	11	6	1	5	--------	10
105	70	4	4	3	8	--------	11
106	49	7	15	9	5	--------	15

TABLE 9.—*Percentage composition, by number, of the six major constituents of the zooplankton collections, by cruise and longitude*

Major constituents	Cruise 2 Jan.–Feb. 1950			Cruise 5 June–Aug. 1950			Cruise 7 Oct.–Nov. 1950	Cruise 8 Jan.–Mar. 1951		
	172° W.[1]	158° W.[2]	Total	172° W.[3]	158° W.	Total	158° W.	172° W.[4]	158° W.[5]	Total[6]
Copepoda	58.9	56.2	57.4	56.3	53.0	54.9	60.2	58.6	58.0	58.4
Chaetognatha	16.7	14.0	15.2	8.3	10.0	9.0	12.0	12.4	12.2	13.5
Tunicata	5.6	8.2	7.1	5.6	5.6	5.6	4.7	6.1	5.3	5.3
Euphausiacea	3.9	9.1	6.8	4.9	3.5	4.3	3.0	4.6	5.9	5.6
Siphonophora	4.2	2.9	3.5	5.0	3.4	4.3	4.3	5.2	4.0	4.3
Foraminifera	2.5	1.3	1.8	7.7	9.9	8.6	3.0	1.6	4.8	2.5
Miscellaneous	8.2	8.3	8.2	12.2	14.6	13.3	12.8	11.5	9.8	10.4

[1] Includes stations 1 to 26.
[2] Includes stations 30 to 53.
[3] Includes stations 1 to 27.
[4] Includes stations 77 to 106.
[5] Includes stations 1 to 26.
[6] Includes stations 1 to 106, all longitudes.

The uniform composition of the zooplankton, as shown by our measurements, indicates the existence of a stable ecological balance among the various components of the plankton and between them and their environment. This uniformity, or stability, is doubtless the result of a complex interaction of factors. The physical and chemical factors of the environment throughout the range sampled are rather homogeneous and, perhaps while capable of effecting differences in total abundance of organisms, do not provide sufficient variations to promote major differences in the composition of populations. The relative absence of irregularly occurring swarms of larval and adult forms may account for some of the uniformity. It is reasonable to assume that, despite the great species differences that may occur (Wilson 1942), there is a particular niche in this ecosystem of the tropical and subtropical Pacific which will support a certain number of copepods, and another which will accommodate a certain number of chaetognaths, and so forth. The uniformity of the data on plankton composition also argues that the collecting method and its uniformity of application were appropriate for producing repeatable results.

ZOOPLANKTON AS FOOD

It is generally recognized that neither an enumeration of organisms present nor a total-volume measurement shows the actual food value of a plankton sample. Food value could be estimated by chemical analysis of each sample, but this procedure is hardly practical when large numbers of samples must be examined. Sufficient work has been done on the chemical composition of the major zooplankton types to show that they vary widely in nutritive value among types and even within types for different localities.

According to Bigelow and Sears (1939), the separation of the crustaceans and chaetognaths from the other types of zooplankton permits an approximate division of the zooplankton into (1) more nutritive forms which may be important as fish food and (2) forms of little or no nutritive value, such as the tunicates and siphonophores. In our collections, the crustacean-chaetognath group averages 70 to 80 percent by number.

Nakai (1942) has shown that plankton animals from the southern part of the Sea of Japan generally contain less fat than those of northern areas. The inference is made that in the warmer waters to the south, the scarcity of phytoplankton, particularly of diatoms with their rich oil reserves, prevents the accumulation of fat by the zooplankton. Clarke (1940) found that in the western Atlantic the plankton of coastal water had a higher percentage of organic matter than that of continental-slope or Sargasso-Sea water. Subtropical plankton in general had a low organic content. It is possible, therefore, that while three-fourths by number, and a smaller fraction by volume, of the zooplankton of the central Pacific is theoretically nutritious, its actual food value in calories may be less than for similar organisms of higher latitudes.

The Pacific Oceanic Fishery Investigations is conducting a study of the food of tunas. The results to date show that a variety of zooplankton forms are utilized directly as food by these fish. For example, representatives of the following groups have been captured in our plankton nets and have also been found among the stomach contents of maturing and adult yellowfin tuna (Reintjes and King 1953):

mysids
euphausiids
amphipods
stomatopod larvae
shrimps
palinurid larvae
brachyuran larvae
heteropods
pteropods
cephalopod young
tunicates
fish young

References have been previously cited (p. 111) emphasizing the importance of plankton in the food of juvenile tunas.

ABUNDANCE OF THE ZOOPLANKTON

Estimated numbers and volumes of zooplankton, times of sampling, and amounts of water strained, are given in tables 1, 2, 3, and 4. Variations in abundance with latitude are demonstrated by the histograms of figures 4, 5, 6, 7, and 8. The results are briefly summarized in tables 10 and 11.

TABLE 10.—*Areas of greatest abundance of zooplankton, by cruise and longitude*

Zooplankton	Cruise 2		Cruise 5		Cruise 7	Cruise 8	
	172° W.	158° W.	172° W.	158° W.	158° W.	172° W.	158° W.
Greatest estimated number/m.^{3}	109	83	107	93	75	73	90
Latitude of greatest estimated number	0°	5° S.	1° S.	3° N.	2° N.	1° N.	1° S.
Greatest displacement volume, cc./m.^{3}	.0826	.0911	.0742	.0880	.0741	.0548	.0666
Latitude of greatest displacement volume	0°	1° S.	1° S.	0°	2° N.[1]	2° N.	5° S.
Boundaries of rich area (estimated numbers)	2° N.–0°	3° N.–5° S.	4° N.–3° S.	5° N.–0°	6° N.–2° N.	6° N.–1° S.	1° S.–6° S.
Boundaries of rich area (displacement volumes)	2° N.–2° S.	3° N.–1° S.	1° N.–3° S.	5° N.–0°	6° N.–2° N.	5° N.–1° S.	1° S.–5° S.
Latitudinal range of collection	24° N.–5° S.	19° N.–5° S.	27° N.–5° S.	21° N.–5° S.	20½° N.–2° S.	21° N.–14½° S.	21° N.–7° S.

[1] Sample at 19° N. latitude was greatest in volume but was atypical, as it contained a highly unusual number and volume of amphipods. (See table 3.)

TABLE 11.—*Numbers and volumes of zooplankton organisms as related to equatorial currents and latitudes*

[Data from the six major sections of cruises 2, 5, and 8, which crossed the Equator on 158° and 172° W. longitude]

Current	Latitude	Number of observations	Zooplankton organisms	
			Average number per m.^{3}	Average volume, cc. per m.^{3}
North Equatorial Current	27°–18° N.	14	28	0.0184
	17°–11° N.	27	26	.0176
Countercurrent	10°–6° N.	25	32	.0255
South Equatorial Current	5°–1° N.	25	53	.0430
	Equator	5	73	.0605
	1°–5° S.	25	46	.0373
	6°–14° S.	8	34	.0175

In general, at the time and through the range of latitudes sampled (27° N. to 14° S.), the greatest abundance of zooplankton was found in the region of the Equator, between 6° N. and 5° S. latitude. The latitude of peak abundance varied with longitude and cruise. Although not evaluated statistically, there appears in all sections a strikingly parallel variation between the estimated number for each sample and the displacement volume. Because of the disparity in size among the different kinds of zooplankton organisms, numbers are much less meaningful indicators of productivity, or available food, than sample volumes; therefore, our statistical studies have been based solely on volume determinations.

When the varying abundance of zooplankton is reviewed in respect to the presence or absence of a convergence north of the Equator, certain interesting relationships are indicated:

1. When a well-marked convergence is present, the rich zone of zooplankton appears to lie between the Equator and the convergence to the northward (fig. 4, left panel; fig. 5, right panel). The eastern section, cruise 2 (fig. 4, right panel) on which only surface tows were employed, does not conform to this generality. Much of the irregularity in this section, however, is due to differences between samples taken by day and by night.

2. The northern boundary of the rich zone is practically demarcated by the position of the convergence—when it occurs.

3. When a well-marked convergence is lacking, the peaks of abundance—both in number and volume—occur south of the Equator (fig. 5, left panel; fig. 7, right panel).

4. The cruise-8 hydrographic data are not as yet completely processed and the presence or absence of convergences has not been determined for all sections; however, there is no evidence of a convergence along 158° W. longitude (fig. 7, right panel).

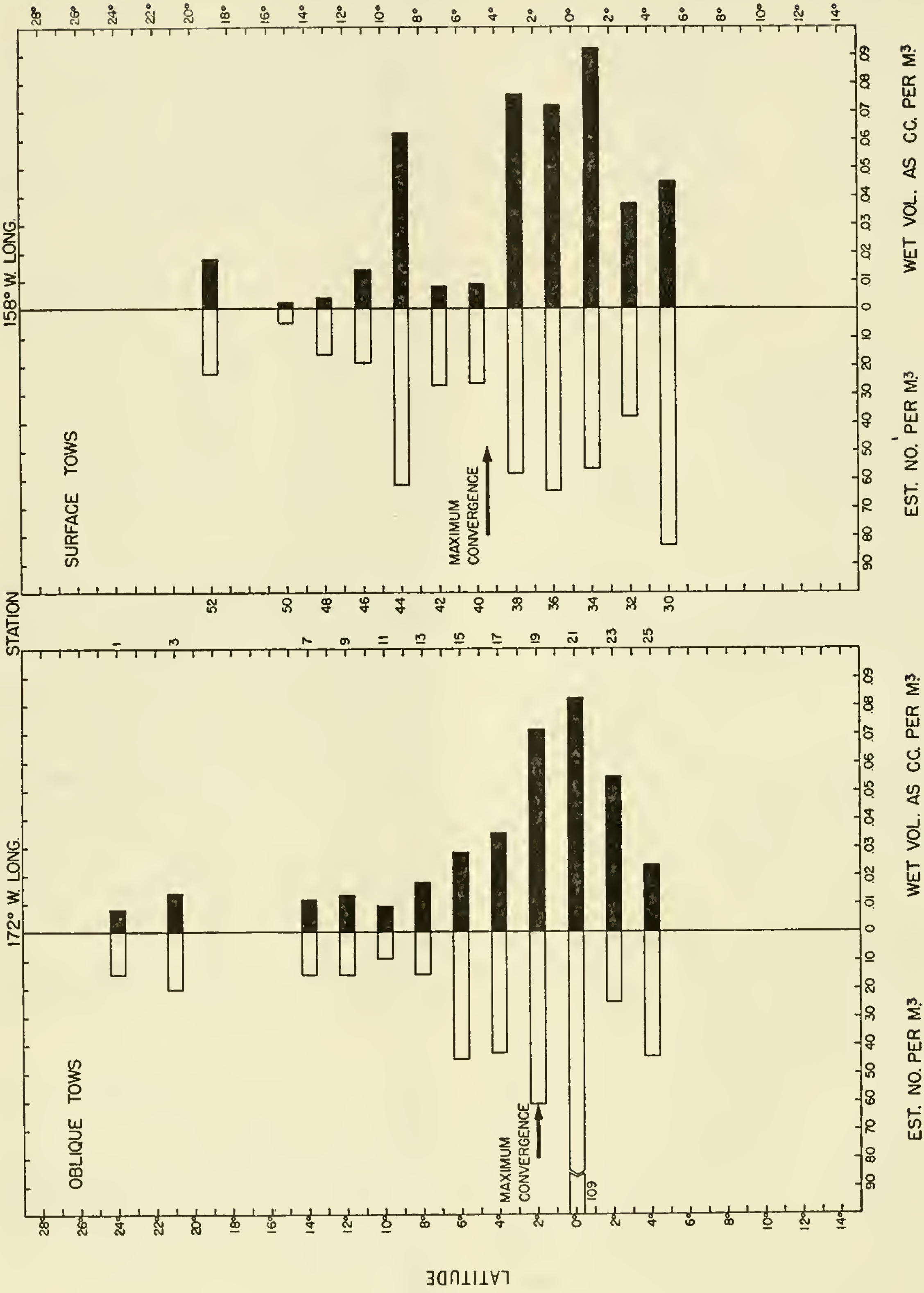


FIGURE 4.—Histograms of zooplankton abundance, as estimated numbers and volumes per m.^{3} of water strained, for cruise-2 stations.

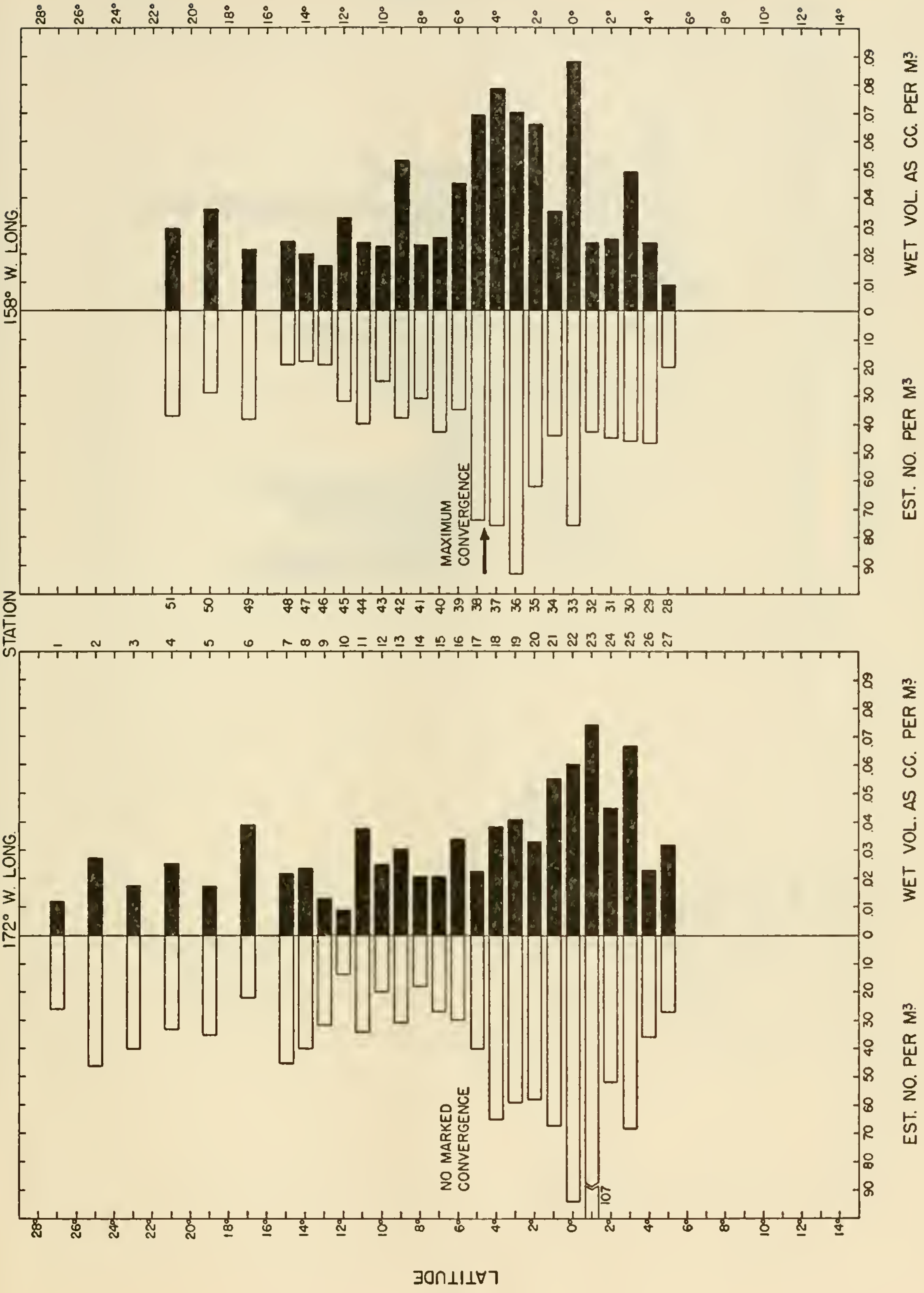


FIGURE 5.—Histograms of zooplankton abundance, as estimated numbers and volumes per m.^{3} of water strained, for cruise-5 stations.

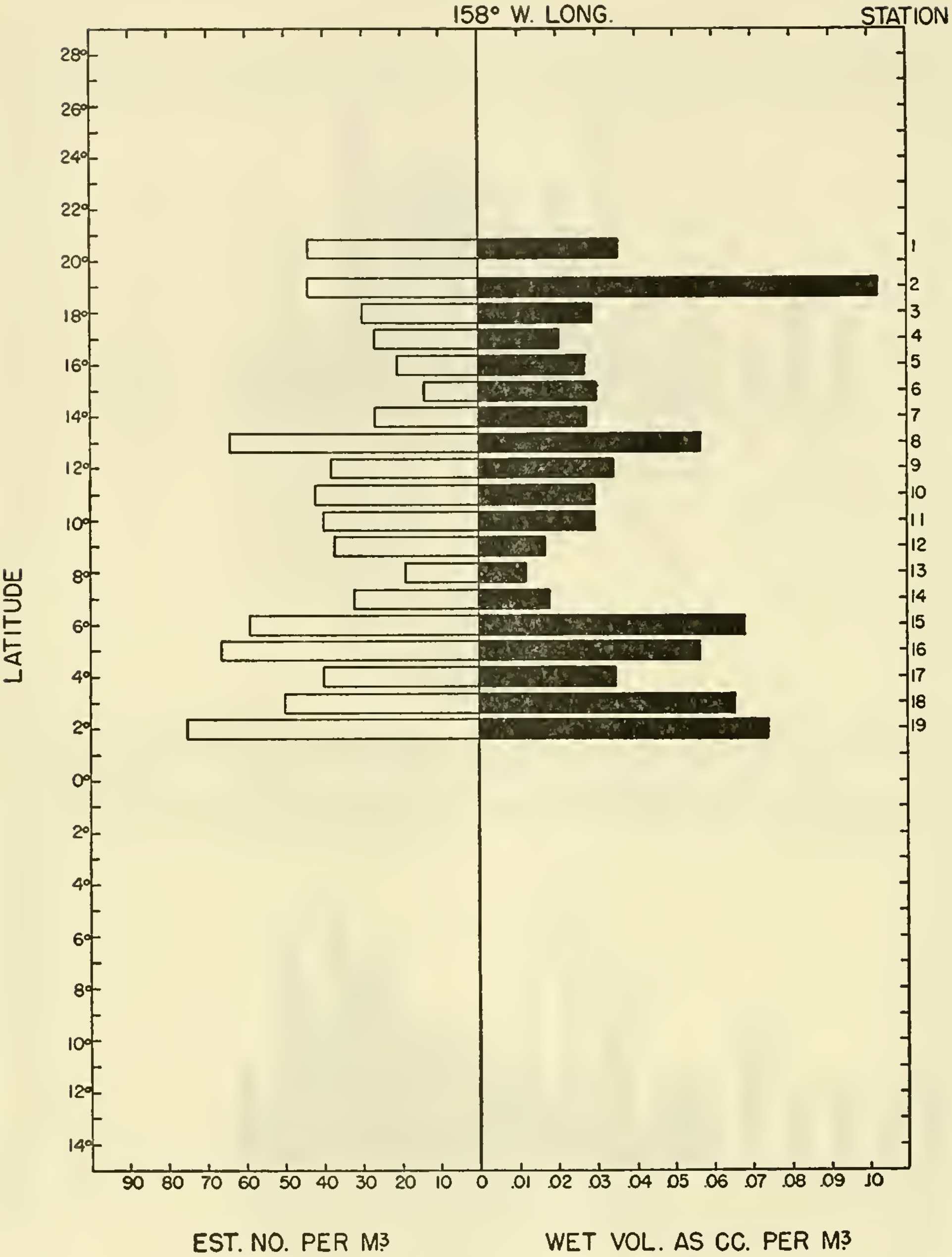


FIGURE 6.—Histogram of zooplankton abundance, as estimated numbers and volumes per m.^{3} of water strained, for cruise-7 stations.

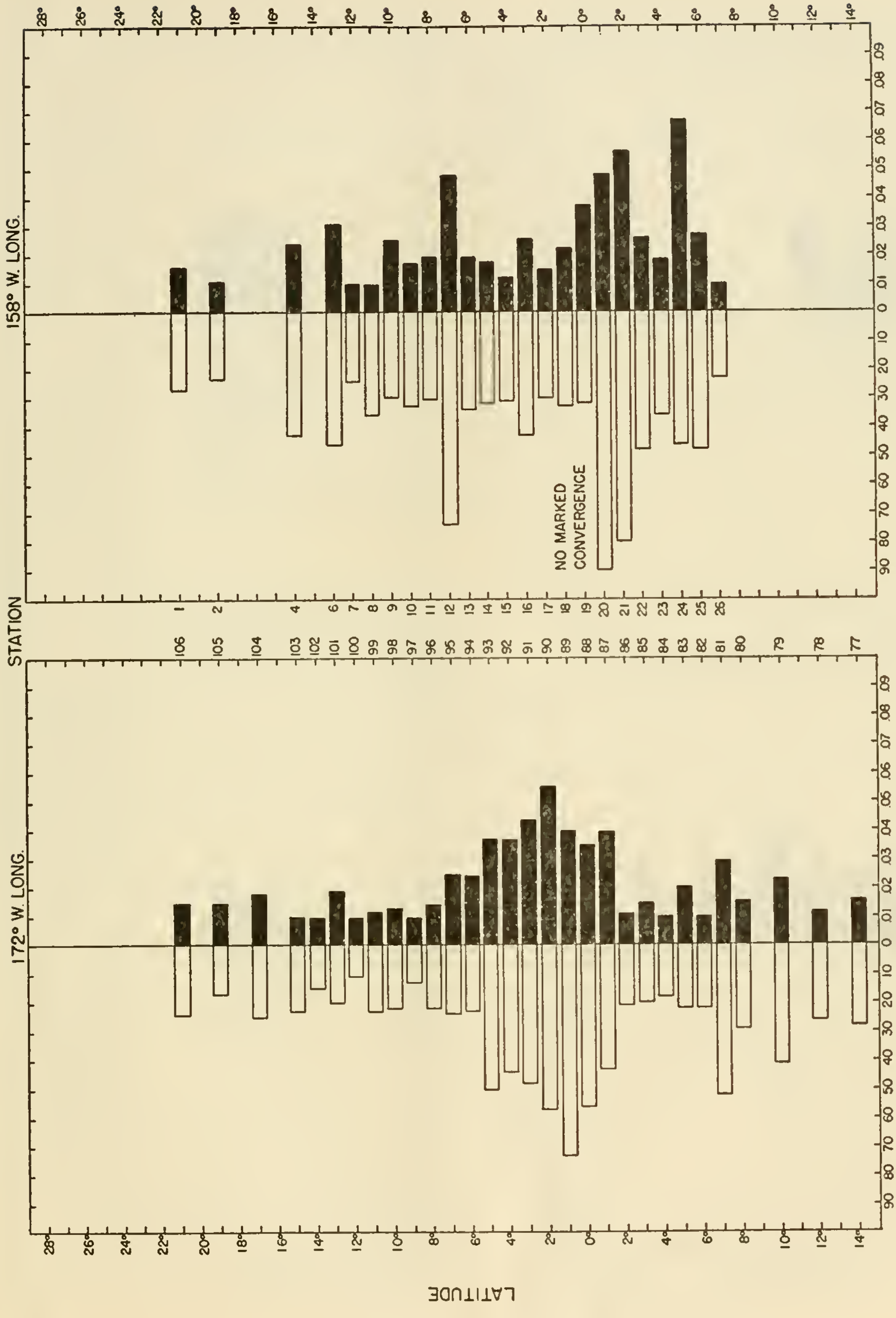


FIGURE 7.—Histograms of zooplankton abundance, as estimated numbers and volumes per m.³ of water strained, for cruise-8 stations on longitudes 158° and 172° W.

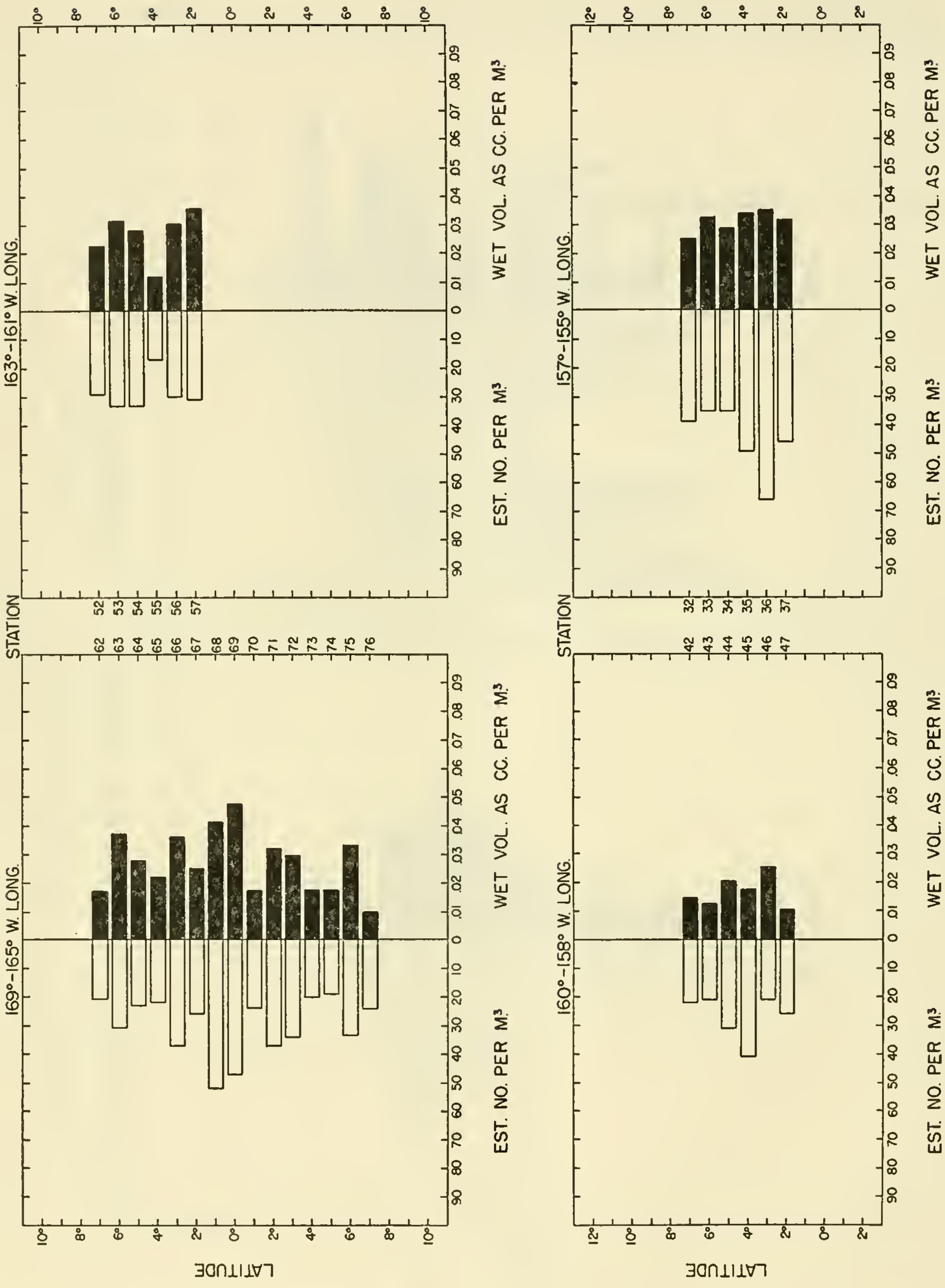


FIGURE 8.—Histograms of zooplankton abundance, as estimated numbers and volumes per m.³ of water strained, for cruise-8 stations located on the short sections between longitudes 155° and 169° W.

EFFECTS OF THE EQUATORIAL CURRENT SYSTEM

The general pattern of the Pacific Equatorial Current system has been described by Sverdrup, Johnson, and Fleming (1942, pp. 708–712). Cromwell (1951 and unpublished ms.[3]), on the basis of recent investigations by this laboratory, suggests certain modifications in the generally accepted ideas pertaining to the details of the circulation. The existence of the equatorial divergence with resultant upwelling of nutrient-rich water, as demonstrated by the *Carnegie* section of 1929 (Sverdrup, et al. 1942), is substantiated by the researches of this laboratory. The presence of a second major divergence at the northern boundary of the Countercurrent has not been confirmed, however. Cromwell concludes, on the basis of the information obtained on three cruises (2, 5, and 8) of the *Hugh M. Smith*, that there is no evidence that any enrichment of the surface layer—as a result of upwelling accompanying a divergence—is occurring at the boundary between the North Equatorial Current and the Countercurrent.

On cruise 2, a sharp temperature discontinuity, together with a local deepening of the thermocline, was found to occur at about 2° N. latitude on the western section and at about 4½° N. latitude on the eastern section (fig. 4). These conditions indicate the presence of a convergence or "front" (Cromwell ms.) in the surface currents. The northern boundary of the South Equatorial Current was discernible at 5½° N. latitude on the western section, but was not well defined on the eastern section. The convergence near 2° N. latitude was entirely within the South Equatorial Current and, therefore, was not associated with the boundary of this current and the Countercurrent as indicated by Sverdrup, et al. (1942, pp. 710, 711) and Arrhenius (1950). A well-defined convergence, as demonstrated by a marked temperature discontinuity and a deepening thermocline, occurred at 4½° N. latitude on the eastern section of cruise 5 (fig. 5) and again was entirely within the South Equatorial Current. An examination of the data from the oceanographic cruises (tables 6 to 8) indicates that the convergence was more pronounced in certain sections than in others and in some it was not strong enough to exhibit the usual signs and may have been entirely lacking, thus permitting the inference that it is shifting and transitory in nature.[4]

Newly upwelled water is at first poorly populated as regards both phytoplankton and zooplankton (Steemann Nielsen 1937). The latter does not benefit directly from the nutrient-rich water but must await the development of a phytoplankton population. In a region of fairly rapid currents, the phytoplankton maximum and the more slowly developing zooplankton maximum would be expected to occur at a considerable distance from each other both in time and space. Steemann Nielsen (1937) reports that in Iceland waters, when conditions for phytoplankton change from bad to good, the capacity for rapid reproduction in phytoplankton enables a few specimens to establish a rich population in 10 days; large quantities of zooplankton do not show up until about a month later. We are not aware of similar population-growth data for the tropics, but we can safely assume that the rate of development here would be considerably more rapid. Nevertheless, it is surprising that in our sampling we found the zooplankton maximum frequently occurring on or very near the site of the upwelling.

Since the days of Hensen and the German Plankton Expedition of 1889, tropical seas have been considered less productive than those of higher latitudes. Explanations for this are usually based on the theory that in the tropics surface heating results in a stable stratification of the sea, thus preventing any vertical mixing by convection which would bring nutrients to the euphotic zone (Delsman 1939; Graham 1941; Sverdrup, et al. 1942, p. 942; Arrhenius 1950). Such thermal stratification does apparently exist throughout much of the tropical, subtropical, and temperate Pacific in areas removed from land influence.

It was learned from the last cruise of the *Carnegie* in 1929, that these generally stable dynamic conditions are disrupted at the Equator by a strong divergence which is accompanied by upwelling. The latter was considered responsible for the enrichment of the surface layers and the production of much higher concentrations of plankton than were found in subtropical and temperate latitudes (Graham 1941). The frequently appearing convergence at 2° to 5° N. latitude also contributes to this apparent greater abundance of life in the equatorial region. Floating organisms with high buoyancy undoubtedly congregate here just as driftwood does along a current rip or other discontinuity zone; zooplankton capable of resisting the downward currents would also tend to concentrate in the surface layers. When a strong convergence has persisted for a sufficient length of time, an area of relatively high-plankton abundance should result, providing rich pasturage for plankton-feeding animals.

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[3] Circulation in a meridional plane in the central equatorial Pacific.

[4] The Equatorial Current system is considerably more complex than indicated here. Details of the circulation at the divergence and the convergence and the causal forces involved, are presently being studied by members of this organization and the Scripps Institution of Oceanography.

The unusual abundance of marine life in the equatorial region has been observed by many expeditions and world travelers while crossing the Pacific. Agassiz and Mayer (1902), in their report on observations and collections of the *Albatross* in the tropical Pacific, state,

> In fact it is evident that pelagic animals are not abundant in regions far from large land masses or where there are no well-defined oceanic currents or counter currents. As soon as one approaches the region of great currents or counter currents, or the coasts of continents and larger islands, the number of animals increases with remarkable suddenness.

Beebe (1926) describes masses of floating debris and the associated wealth of life in a current rip some 200 miles southeast (between 3° and 4° N. latitude) of Cocos Island in the eastern Pacific. Brooks (1934), in reporting his observations on certain relationships between ocean currents and birds, asks why it is that on ocean voyages day after day goes by and no birds or marine life are seen and then suddenly one passes into an area teeming with life. He observed that, as his vessel neared the Equator from the north, bird life increased greatly, as did other marine life such as flying fish, sharks, and whales; then as he crossed the Equator, the zone of abundant life was left behind.

Revelle (1944) points out the agreement between the southern boundary of the Countercurrent and the northern border of the Pacific *Globigerina* ooze area. In reporting on results of the recent Swedish Deep-Sea Expedition, Arrhenius (1950) states in respect to the Pacific,

> The biogenous component and simultaneously the rate of sedimentation increases strongly below the convergence where a biolith, rich in fossils of foraminifera, radiolaria and diatoms is thus deposited. North of the convergence of the Equatorial Counter Current, the share of the biogenous component in the sedimentation decreases and the fossil-rich biolith turns into a clay, poor in fossils and with a low intensity of sedimentation.[5]

As summarized by Herdman (1923),

> It is probable, on the whole, that the distribution and variation of ocean currents have more than latitude or temperature alone to do with any observed scantiness of tropical plankton. These mighty rivers of the ocean in places teem with animal and plant life, and may sweep abundance of food from one region to another in the open sea.

VARIATION IN ZOOPLANKTON ABUNDANCE

The sampling method used in the present study meets the criteria for randomness in most respects, allowing the use of standard methods of statistical analysis. Although the stations were located in systematic order, a random sample was probably obtained of the zooplankton population retained by a meter net with 0.65-mm. apertures from the upper 200 meters of water. There is some doubt, however, as to the type of distribution of the plankton population. Although our results indicate a rather uniform, but very dilute distribution of zooplankton, which would perhaps conform to a Poisson distribution, the majority of workers have reported clumping and lack of uniformity. Snedecor (1946, pp. 42 and 252) states that the requirement of randomness must be adhered to, but normal distribution of the population is a specification that can be considerably relaxed. Of course, there are devices appropriate for analyzing samples from nonnormal distributions. One commonly used method involving a transformation of the data to logarithms, was employed in certain initial tests of the volume data. The results and conclusions obtained were the same, however, as those reached through an analysis of the untransformed data. We assumed, therefore, that the degree of anormality in the zooplankton population would affect our inferences but little, and in this report have chosen to examine and base our conclusions upon tests of the untransformed data. We wish to emphasize the point that all statistical analyses were made on zooplankton volumes rather than on numbers.

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[5] The convergence here referred to by Arrhenius is that which theoretically occurs at the southern boundary of the Countercurrent and, as previously stated, has not been observed by these investigations. We have found the convergence 2° to 3° south of the current boundary and entirely within the South Equatorial Current.

An examination of the histograms in figures 4, 5, 6, 7, and 8 reveals distinct variations in zooplankton abundance with latitude; differences between longitudes and between cruises are not so obvious, however. The hydrographic data obtained coincident with the zooplankton collections also show latitudinal variations in inorganic phosphate, surface and subsurface temperature, oxygen, and thermocline depth (fig. 9). The marked differences between day and night hauls have already been referred to in the discussion of methods. By employing an analysis of variance, we have attempted to determine the significance and magnitude of these space-time variations in zooplankton abundance; by using correlation and multiple-regression analyses we have been able to measure the degree of covariation between zooplankton and these different environmental factors.

Effect of time of sampling

Our sampling method was not specifically designed to evaluate variations among the zooplankton volumes resulting from differences between day and night hauls. An accurate measure of these differences would have required both day and night hauls (preferably within a 24-hour period) at every station. These day-night variations could perhaps have been eliminated by visiting every station at the same time of day or night. In view of the number of stations and the large area covered, neither procedure was practical.

Although on cruises 2, 5, and 8 there was, theoretically, opportunity for the occurrence of equal numbers of day and night collections, it so happened that the day collections outnumbered the night collections. Rarely, however, were more than 2 day stations or 2 night stations occupied consecutively.

An estimate of the importance of the day-night variation, as compared with the latitudinal variation, was obtained from the cruise-5 and cruise-8 data, using an analysis of variance with two criteria of classification (following Snedecor 1946, p. 256). We paired, impartially, successive night and day hauls, where both occurred on the same longitude and on about the same latitude, omitting those stations where two or more day hauls or night hauls were made in succession, and also omitting those stations worked during twilight periods.

An analysis of the cruise-5 volumes (table 12) indicates that for this cruise, there were significant ($P<0.05$) differences between the day and night hauls and also among latitudes. For the cruise-8 volumes (table 13), there were also significant ($P<0.01$) differences between the day and night hauls and among latitudes.

If the means for latitudes are compared using the "least significant difference" calculated according to the method of Johnson (1950, p. 123; $LSD=(t_{.05})\ \sqrt{2s^2/k}$), it is evident that for both cruises the means obtained near the Equator are significantly greater than those to the north or south of the Equator. For example, on cruise 8, the mean volume (0.0513 cc./m.^{3}) for 1° and 2° S. latitude differs from the mean volume (0.0178 cc./m.^{3}) for 8° and 9° N. latitude by a difference of 0.0335, which is considerably greater than the least significant difference, 0.0165.

TABLE 12.—*Cruise 5: Analysis of variance of volumes of paired samples taken by day and by night in about the same latitude*

[Two criteria of classification]

Station Nos.	Latitudes	Volume (cc./m.^{3})		Mean
		Day	Night	
1 and 2	27° and 25° N	0.0118	0.0271	0.0194
5 and 4	19° and 21° N	.0174	.0254	.0214
7 and 8	15° and 14° N	.0216	.0234	.0225
12 and 11	10° and 11° N	.0252	.0374	.0313
15 and 14	7° and 8° N	.0204	.0203	.0204
17 and 16	5° and 6° N	.0226	.0338	.0282
18 and 19	4° and 3° N	.0385	.0410	.0398
21 and 22	1° N. and 0°	.0556	.0604	.0580
24 and 25	2° and 3° S	.0452	.0664	.0558
26 and 27	4° and 5° S	.0230	.0315	.0272
29 and 30	4° and 3° S	.0239	.0490	.0370
32 and 33	1° S. and 0°	.0239	.0880	.0560
35 and 36	2° and 3° N	.0658	.0701	.0680
38 and 39	5° and 6° N	.0691	.0449	.0570
41 and 42	8° and 9° N	.0230	.0531	.0380
44 and 45	11° and 12° N	.0242	.0327	.0284
47 and 48	14° and 15° N	.0201	.0246	.0224
50 and 51	19° and 21° N	.0357	.0289	.0323
Mean		.0315	.0421	

Least significant difference for latitudinal means=.0268

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Times	1	0.00101336	0.00101336*	6.28	<0.05
Latitudes	17	.00814675	.00047922*	2.97	<0.05
Discrepancy	17	.00274379	.00016140		
Total	35	.01190390			

*Indicates a significant ($P<0.05$) mean square value.

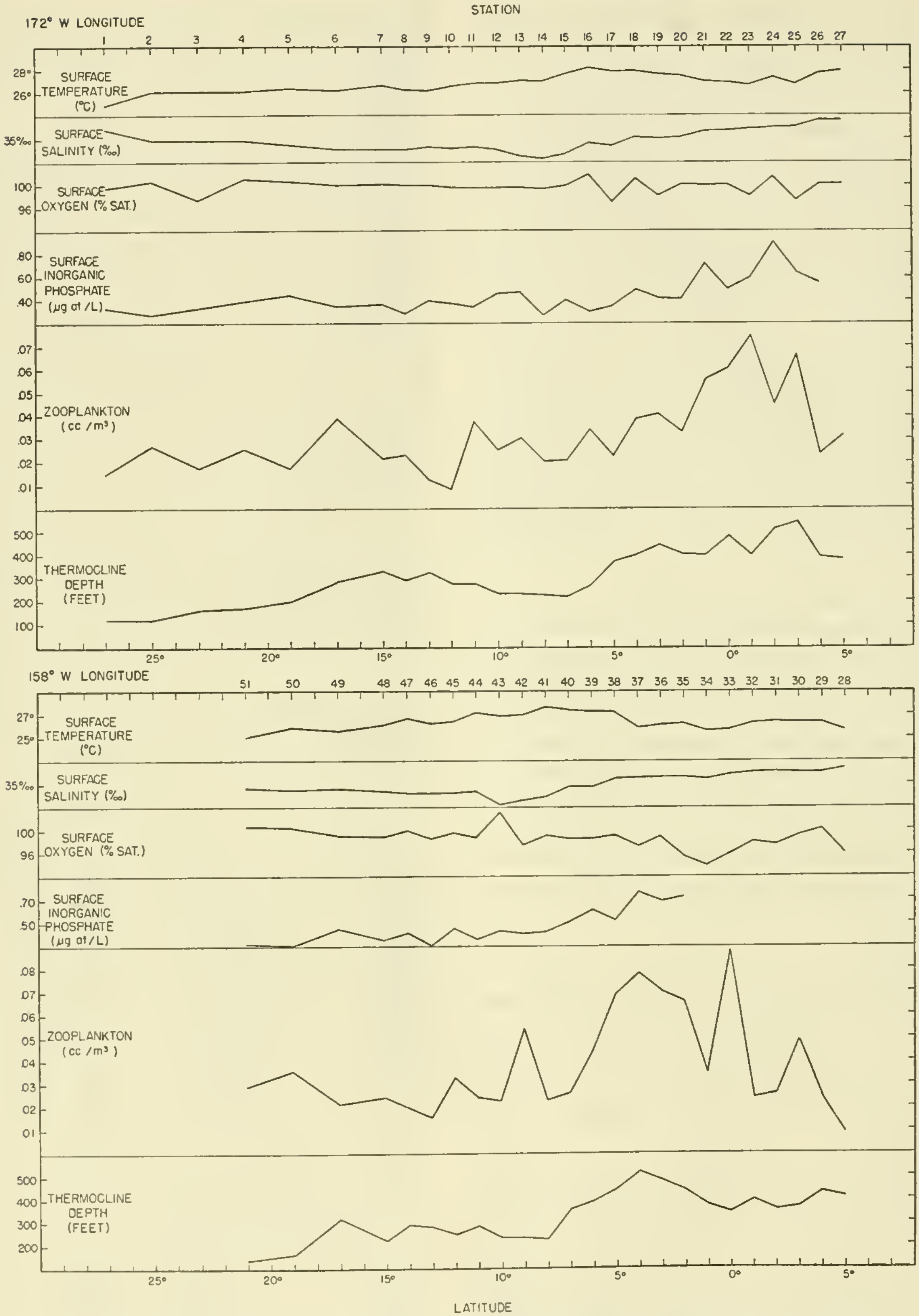

FIGURE 9.—Variations in temperature, salinity, oxygen, inorganic phosphate, thermocline depth, and zooplankton volume along 158° and 172° W. long. as found on cruise 5, *Hugh M. Smith*, June–August 1950.

TABLE 13.—*Cruise 8: Analysis of variance of volumes of paired samples taken by day and by night in about the same latitude*

[Two criteria of classification]

Station Nos.	Latitudes	Volume (cc./m.³)		Mean
		Day	Night	
2 and 1	19° and 21° N	0.0105	0.0154	0.0130
4 and 6	14½° and 13° N	.0236	.0310	.0273
8 and 9	11° and 10° N	.0093	.0251	.0172
10 and 11	9° and 8° N	.0166	.0190	.0178
13 and 14	6° and 5° N	.0186	.0174	.0180
15 and 16	4° and 3° N	.0118	.0255	.0186
18 and 19	1° N. and 0°	.0220	.0370	.0295
20 and 21	1° and 2° S	.0478	.0558	.0513
23 and 24	4° and 5° S	.0178	.0666	.0422
33 and 32	6° and 7° N	.0325	.0251	.0288
36 and 35	3° and 4° N	.0348	.0340	.0344
43 and 44	6° and 5° N	.0126	.0204	.0165
45 and 46	4° and 3° N	.0177	.0254	.0216
52 and 53	7° and 6° N	.0224	.0313	.0268
55 and 54	4° and 5° N	.0118	.0276	.0197
62 and 63	7° and 6° N	.0170	.0368	.0269
65 and 66	4° and 3° N	.0118	.0359	.0238
70 and 69	1° S. and 0°	.0172	.0473	.0322
73 and 72	4° and 3° S	.0175	.0295	.0235
76 and 75	7° and 6° S	.0100	.0332	.0216
78 and 79	12° and 10° S	.0115	.0226	.0170
82 and 81	6° and 7° S	.0100	.0291	.0196
84 and 83	4° and 5° S	.0101	.0202	.0152
86 and 87	2° and 1° S	.0109	.0394	.0252
89 and 90	1° and 2° N	.0398	.0548	.0473
94 and 93	6° and 5° N	.0242	.0369	.0306
97 and 98	9° and 10° N	.0094	.0127	.0110
100 and 101	12° and 13° N	.0097	.0192	.0144
104 and 105	17° and 19° N	.0181	.0145	.0163
Mean		.0182	.0306	

Least significant difference for latitudinal means=.0165

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Times	1	0.00225564	0.00225564**	34.60	<0.01
Latitudes	28	.00553218	.00019758**	3.03	<0.01
Discrepancy	28	.00182531	.00006519		
Total	57	.00961313			

**Indicates a highly significant ($P<0.01$) mean square value.

Thus, despite the important variation resulting from diurnal migration of the zooplankton, there still remain in our data significant differences among latitudes. Zooplankton populations occurring near the Equator are significantly greater in abundance than those of adjoining areas.

Variations between cruises, latitudes, and longitudes

To examine differences between cruises and between longitudes and to inspect further the differences among latitudes, an analysis of variance with multiple classification as outlined by Snedecor (1946, pp. 304–309) was utilized, employing as many of the cruise-5 and cruise-8 data as were available for similar latitudes and longitudes (table 14). The analysis is of the same general type as that used by Winsor and Clarke (1940) in their study of variation in the catch of plankton nets.

TABLE 14.—*Analysis of variance of volumes (cc./m.³) of zooplankton samples collected on cruises 5 and 8*

[Three criteria of classification]

Latitude	Series A (172° W. longitude)		Series B (158° W. longitude)		Mean
	Cruise 5	Cruise 8	Cruise 5	Cruise 8	
21° N	0.0254	0.0145	0.0289	0.0154	0.0210
19° N	.0174	.0145	.0357	.0105	.0195
15° N	.0216	.0100	.0246	.0236	.0200
13° N	.0125	.0192	.0158	.0310	.0196
12° N	.0084	.0097	.0327	.0094	.0150
11° N	.0374	.0115	.0242	.0093	.0206
10° N	.0252	.0127	.0225	.0251	.0214
9° N	.0301	.0094	.0531	.0166	.0273
8° N	.0203	.0139	.0230	.0190	.0190
7° N	.0204	.0244	.0258	.0477	.0296
6° N	.0338	.0242	.0449	.0186	.0304
5° N	.0226	.0369	.0691	.0174	.0365
4° N	.0385	.0367	.0783	.0118	.0413
3° N	.0410	.0435	.0701	.0255	.0450
2° N	.0330	.0548	.0658	.0146	.0420
1° N	.0556	.0398	.0347	.0220	.0380
0°	.0604	.0345	.0880	.0370	.0550
1° S	.0742	.0394	.0239	.0478	.0463
2° S	.0452	.0109	.0253	.0558	.0343
3° S	.0664	.0146	.0490	.0257	.0389
4° S	.0230	.0101	.0239	.0178	.0187
5° S	.0315	.0202	.0087	.0666	.0318
Mean	.0338	.0230	.0394	.0258	

Least significant difference for latitudinal means=.0218

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Main effects:					
Series (S)	1	0.00039964	0.00039964	1.67	>0.05
Cruises (C)	1	.00329280	.00329280**	13.79	<0.01
Latitudes (L)	21	.01052548	.00050121*	2.10	<0.02
First-order interactions:					
S×C	1				
S×L	21				
C×L	21	.01528396	.00023881		
Second-order interaction:					
S×C×L	21				
Total	87	.02950188			

* Indicates a significant ($P<0.05$) mean square value.

** Indicates a highly significant ($P<0.01$) mean square value.

The analysis was first carried out in full to determine the significance of the first-order interactions. As these proved to be nonsignificant, they were pooled (following Kendall 1948, p. 201) with the second-order interaction to give a new sum of squares with 64 degrees of freedom and a new mean square which was then used as the error term for testing the main effects. The following observations may be made from the tests of significance:

1. No significant differences ($P>0.05$) are demonstrated between the means for series (longitudes) (0.0284 cc./m.³ for 172° W. longitude, and 0.0326 cc./m.³ for 158° W. longitude).
2. Significant differences ($P<0.01$) are demonstrated between the means for cruises (0.0366 cc./m.³ for cruise 5 and 0.0244 cc./m.³ for cruise 8).
3. Significant differences ($P<0.02$) are demonstrated among the means for latitudes (these vary from 0.0550

cc./m.^{3} at the Equator to 0.0150 cc./m.^{3} at 12° N. latitude).

In this analysis no attempt has been made to isolate the component of variance resulting from time of day at which the hauls were made, and the data are insufficient for a 4-way analysis. In table 14, however, the night samples are rather evenly distributed throughout; e. g., the column for series A, cruise 5, contains 8 night hauls and 1 twilight haul; series A, cruise 8, contains 7 night hauls and 4 twilight hauls; series B, cruise 5, contains 8 night hauls and 2 twilight hauls; and series B, cruise 8, contains 9 night hauls and no twilight hauls. As a consequence we might assume that the day-night variation would tend to cancel out.

To test this assumption we have utilized the values given in table 14, and at the expense of considerable loss of data, we have constructed two 3-way tables, one including only day samples (table 15) and the other only night samples (table 16). An analysis of the day samples reveals quite different results than does an analysis of the night samples or of the combined day and night samples. For the day samples we find no significant differences ($P>0.05$) between series (longitudes), between cruises, or among latitudes. An analysis of the night samples provides the same conclusions as were derived from the combined day and night samples, there being no significant differences ($P>0.05$) between series (longitudes) but highly significant differences ($P<0.01$) between cruises and among latitudes.

Table 15.—*Analysis of variance of volumes (cc./m.^{3}) of zooplankton samples taken in day hauls, cruises 5 and 8*

[Latitudes grouped to provide a value for each column; three criteria of classification]

Latitudes	Series A (172° W. longitude)		Series B (158° W. longitude)		Mean
	Cruise 5	Cruise 8	Cruise 5	Cruise 8	
15° and 13° N	0.0216	0.0100	0.0158	0.0236	0.0178
12° and 11° N	.0084	.0097	.0242	.0094	.0129
10° and 9° N	.0252	.0094	.0225	.0166	.0184
7° and 6° N	.0204	.0242	.0258	.0477	.0295
5° and 4° N	.0385	.0367	.0783	.0118	.0413
3° and 2° N	.0330	.0435	.0658	.0146	.0392
1° N. and 0°	.0556	.0398	.0347	.0220	.0380
1° and 2° S	.0742	.0109	.0239	.0478	.0392
3° and 4° S	.0230	.0146	.0239	.0257	.0218
Mean	.0333	.0221	.0350	.0244	----------

Least significant difference for latitudinal means=.0233

Table 15.—*Analysis of variance of volumes (cc./m.^{3}) of zooplankton samples taken in day hauls, cruises 5 and 8*—Continued

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Main effects:					
Series (S)	1	0.00003481	0.00003481	0.14	>0.05
Cruises (C)	1	.00107584	.00107584	4.20	>0.05
Latitudes (L)	8	.00395996	.00049500	1.93	>0.05
First-order interactions:					
S×C	1	.00640043	.00025602	-------	-------
S×L	8				
C×L	8				
Second-order interaction:					
S×C×L	8				
Total	35	.01147104	------------	-------	-------

Table 16.—*Analysis of variance of volumes (cc./m.^{3}) of zooplankton samples taken in night hauls, cruises 5 and 8*

[Latitudes grouped to provide a value for each column; three criteria of classification]

Latitudes	Series A (172° W. longitude)		Series B (158° W. longitude)		Mean
	Cruise 5	Cruise 8	Cruise 5	Cruise 8	
13°, 12°, and 11° N	0.0374	0.0192	0.0327	0.0310	0.0301
10°, 9° N	.0301	.0127	.0531	.0251	0302
8°, 7°, and 6° N	.0338	.0139	.0449	.0190	.0279
5°, 4°, and 3° N	.0410	.0369	.0701	.0255	.0434
2°, 1° N., and 0°	.0604	.0548	.0880	.0370	.0600
1°, 2°, and 3° S	.0664	.0394	.0490	.0558	.0526
Mean	.0448	.0295	.0563	.0322	----------

Least significant difference for latitudinal means=.0159

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Main effects:					
Series (S)	1	0.00030246	0.00030246	2.67	>0.05
Cruises (C)	1	.00233248	.00233248**	20.62	<0.01
Latitudes (L)	5	.00364125	.00072825**	6.44	<0.01
First-order interactions:					
S×C	1	.00180978	.00011311	-------	-------
S×L	5				
C×L	5				
Second-order interaction:					
S×C× L	5				
Total	23	.00808597	------------	-------	-------

**Indicates a highly significant ($P<0.01$) mean square value.

Although it has been possible to utilize only a portion of the data, the differences between cruises and among latitudes may be regarded as real, for they have been demonstrated not only in table 14 where the day-night component was present, but also in the last analysis, table 16, where the day-night component was removed. The evidence that there is less latitudinal variation in the day samples than in the night samples introduces a new feature and reveals another possible source of variation in the data. The cause, or causes, of this phenomenon, if real, are as yet obscure to the authors, but may be related to differences in basic productivity, depth of thermocline, or other factors of the environment.

In summary, through the foregoing analyses, we have demonstrated that the rich zooplankton catches from near the Equator were significantly greater than those of higher latitudes. We have learned also that there was little difference between the populations along the two longitudes, 172° W. and 158° W., over the range of latitudes sampled. We can state with assurance that there was a distinct difference between the amount of zooplankton taken on the two cruises, 5 and 8. The mean for cruise 5 (0.0366 cc./m.^{3}) conducted during the northern summer, was greater than that for cruise 8 (0.0244 cc./m.^{3}) conducted during the winter; therefore, a seasonal difference is suggested.

CORRELATIONS WITH ENVIRONMENTAL FACTORS

Some of the hydrographic data obtained on cruises of the *Hugh M. Smith* have been published (Cromwell 1951), and since the Pacific Oceanic Fishery Investigations plans to publish the hydrographic data on which these correlations are based, we have not included the data in this paper. Variations in certain features of the surface layer as measured on cruise 5, and graphically portrayed in figure 9, may be summarized as follows:

1. Surface inorganic phosphates—high concentrations of 0.80 to 0.90 μg at./L. were found in the immediate vicinity of the Equator; values decreased to the northward and southward to lows of 0.30 to 0.40 μg at./L.
2. Surface temperature—highest water temperatures, about 28° C., were recorded for latitudes 6° to 8° N.; temperature decreased gradually to the northward and to the southward, reaching 24° to 25° C.
3. Dissolved oxygen (percent saturation at surface)—ranged from 94 percent near the Equator to 102 percent at higher latitudes.
4. Thermocline depth—varied from about 120 feet in the north to over 500 feet in the region of the convergence.

Employing cruise-5 data,[6] a method of correlation analysis (following Snedecor 1946, p. 138) was used to examine the relation between zooplankton volumes and these environmental factors. The results, summarized in table 17, point out the following:

1. Statistically significant ($P<0.01$) positive correlations between zooplankton volume and inorganic phosphates at the surface, at the 100-meter depth, and at depths midway to the top of the thermocline;
2. Statistically nonsignificant ($P>0.05$) correlations between zooplankton volume and temperature, whether at the surface, the 100-meter depth, or at depths midway to the top of the thermocline;
3. Statistically significant negative correlations between zooplankton volume and oxygen (as percent saturation) at the surface ($P<0.05$), at the 100-meter depth ($P<0.01$), and at depths midway to the top of the thermocline ($P<0.01$);
4. Statistically significant ($P<0.01$) correlations between zooplankton volume and depth to the top of the thermocline.

In most ecological investigations it has been found that all factors examined are more or less interrelated, variations in one factor having an influence, either direct or indirect, on all the other factors (Riley 1939a). The multiple-regression method makes corrections for such interactions, and in a three-variate analysis tests the relation of a pair of variates irrespective of the influence of a third.

TABLE 17.—*Correlations of zooplankton abundance, as wet volumes, and certain environmental factors, cruise 5*

Variates		Degrees of freedom	Correlation coefficient (r)	P
X_1	X_2			
Inorganic phosphates (μg at./L.) at surface.	Zooplankton wet volumes.	41	0.655^{**}	<0.01
Inorganic phosphates (μg at./L.) at 100 m. depth.	do	41	0.580^{**}	<0.01
Inorganic phosphates (μg at./L.) at depths midway to thermocline.	do	41	0.730^{**}	<0.01
Temperature (° C.) at surface	do	49	0.008	>0.05
Temperature (° C.) at 100 m. depth.	do	49	0.227	>0.05
Temperature (° C.) at depths midway to thermocline.	do	49	−0.065	>0.05
Oxygen (percent saturation) at surface.	do	49	-0.291^{*}	<0.05
Oxygen (percent saturation) at 100 m. depth.	do	49	-0.834^{**}	<0.01
Oxygen (percent saturation) at depths midway to thermocline.	do	49	-0.489^{**}	<0.01
Thermocline depth (feet)	do	49	0.566^{**}	<0.01

** Indicates a highly significant correlation.
* Indicates a significant correlation.

In the correlation analyses a positive relation between zooplankton volumes and temperature at the 100-meter depth was indicated (table 17), but, being below the 0.05 level of probability, it was not considered statistically significant. It seemed of interest to examine the relation of zooplankton and temperature at the 100-meter level independent of variation with inorganic phosphate. A multiple regression analysis (following Snedecor 1946, pp. 340–373) was therefore carried out employing cruise-5 data, treating zooplankton volumes (cc./m.^{3}) as the Y variate, inorganic phosphates (μg at./L) at 100 meters as the X_1 variate, and temperatures (°C.) at 100 meters as the X_2 variate.

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[6] Since different methods of towing and nets of different mesh size were used on cruise 2, and since the hydrographic data of cruise 8 are not as yet entirely processed, we have used cruise-5 data for the correlation analyses.

The following multiple regression equation was obtained:

$$Y = 0.0484X_1 + 0.0023X_2 - 0.044969.$$

The first partial regression coefficient ($b_{Y1 \cdot 2} = 0.0484$; $t = 5.232$, $P < 0.001$, at 40 degrees of freedom) and the first partial correlation coefficient ($r_{Y1 \cdot 2} = 0.638$; $P < 0.01$) are highly significant, showing that there is a positive relation between zooplankton volumes and inorganic phosphates, independent of the variation with temperature, at the 100-meter level. This conclusion was expected from the previous correlation analysis. The second partial regression coefficient ($b_{Y2 \cdot 1} = 0.0023$; $t = 2.987$, $P < 0.01$, at 40 degrees of freedom) and the second partial correlation coefficient ($r_{Y2 \cdot 1} = 0.423$; $P < 0.01$) are also highly significant, showing that there is also a positive relation between zooplankton volumes and temperature, independent of variation with inorganic phosphate, at the 100-meter level. This conclusion is of interest since it indicates a much higher degree of covariation between zooplankton and temperature, than was revealed by the previous correlation analysis.

We have shown that the abundance of zooplankton in the central Pacific is correlated with inorganic phosphates, temperature, dissolved oxygen, and thermocline depth. We do not believe, though, that the abundance of zooplankton is in any way limited by the conditions of temperature, oxygen, or thermocline depth prevailing throughout the region. The relationships between zooplankton and these three environmental factors, as indicated by the statistical correlations, are most likely independent variations due to common causes. Zooplankton is more directly linked with phosphate, however, through the phosphate→phytoplankton→zooplankton relation. Therefore, the causal agent for these several variations examined is directly or indirectly the Equatorial Current system, principally the divergence at the Equator which brings to the surface water that is relatively low in temperature, low in oxygen content, but high in chemical nutrients, and the convergence to the northward which results in a deepening of the thermocline and a possible concentration of the plankton.

Other investigators have found essentially similar correlations between plankton and these environmental factors. Marshall and Orr (1927) observed in the Clyde Sea area that where animal life was rich, phosphates were high, but dissolved oxygen and pH were low. Hardy and Gunther (1935) found in the Pacific that numbers of zooplankton were positively correlated with phosphate values. Jesperson (1935) states that there is a direct relation between quantities of nitrate and phosphate and macroplankton. Leavitt (1938) found in the Atlantic Basin a correlation between temperature, salinity, and density, and the vertical distribution of zooplankton; a negative correlation was found between oxygen and zooplankton. Graham (1941) reports that differences in productivity in the Pacific, as measured by plankton dry weight, are correlated with the concentration of phosphate.

COMPARISON WITH ZOOPLANKTON ABUNDANCE OF OTHER REGIONS

To facilitate the comparison of our data with that of other regions, we have calculated average numbers and volumes (table 11) which are representative of the quantity of zooplankton in different latitudinal zones of the central Pacific. It is a difficult task, however, to reduce to comparable terms plankton data which have been obtained by different investigators, using different methods, at different seasons, and with results expressed in different units. In surveying a considerable fraction of the great bulk of available literature on quantitative plankton sampling, we found only a few reports that have enough in common with our own work to permit a comparison of the results.

In Graham's report (1941) on plankton collected by the *Carnegie* along a series of stations extending from San Francisco to Samoa, he states, "In the open Pacific Ocean from September to November 1929, there was a greater production of total plankton in the tropics between latitudes 20° N. and 11° S. than between latitudes 20° and 34° N." The richest collection of this section (fig. 10) was taken at 13° N. latitude, but was considered atypical since it consisted largely of salps.

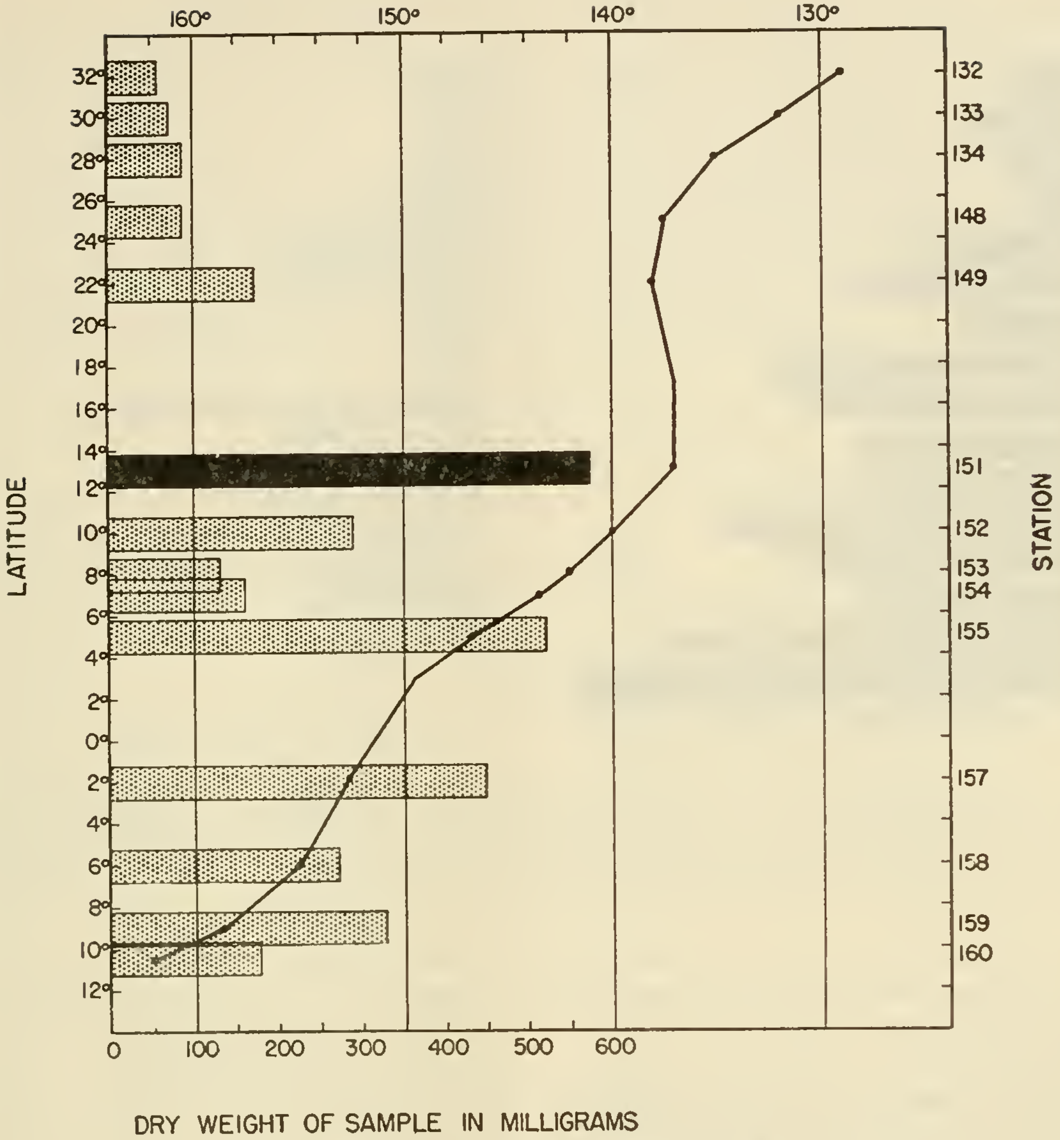

FIGURE 10.—Station positions and zooplankton abundance (as dry weight of sample in milligrams) found on the last cruise of the *Carnegie* in 1929 (data from Graham 1941).

The sample ranking second in dry weight came from 5°30′ N. latitude and the third-ranking sample from 2° S. latitude. These results, while based on a different method of analysis, are in general agreement with our own observations.

The Japanese have carried on extensive plankton investigations in waters adjacent to the Palau Islands and in the area between the Palaus and New Guinea. Results from the studies of Haneda (1942) and Tokioka (1942) are illustrated in figure 11. Although these data are rather limited in scope, the samples of Tokioka show quite definitely the influence of enrichment near the Equator.

These surveys and the work of the *Carnegie* are the only north-south plankton studies that we are aware of in the equatorial Pacific, other than our own. Unfortunately, the absolute values obtained in them cannot be compared with our results, but the generally similar variations with latitude are of interest.

While crossing the Pacific from Panama to the Indo-Pacific region, the *Dana* expedition made plankton tows at frequent intervals. Jesperson

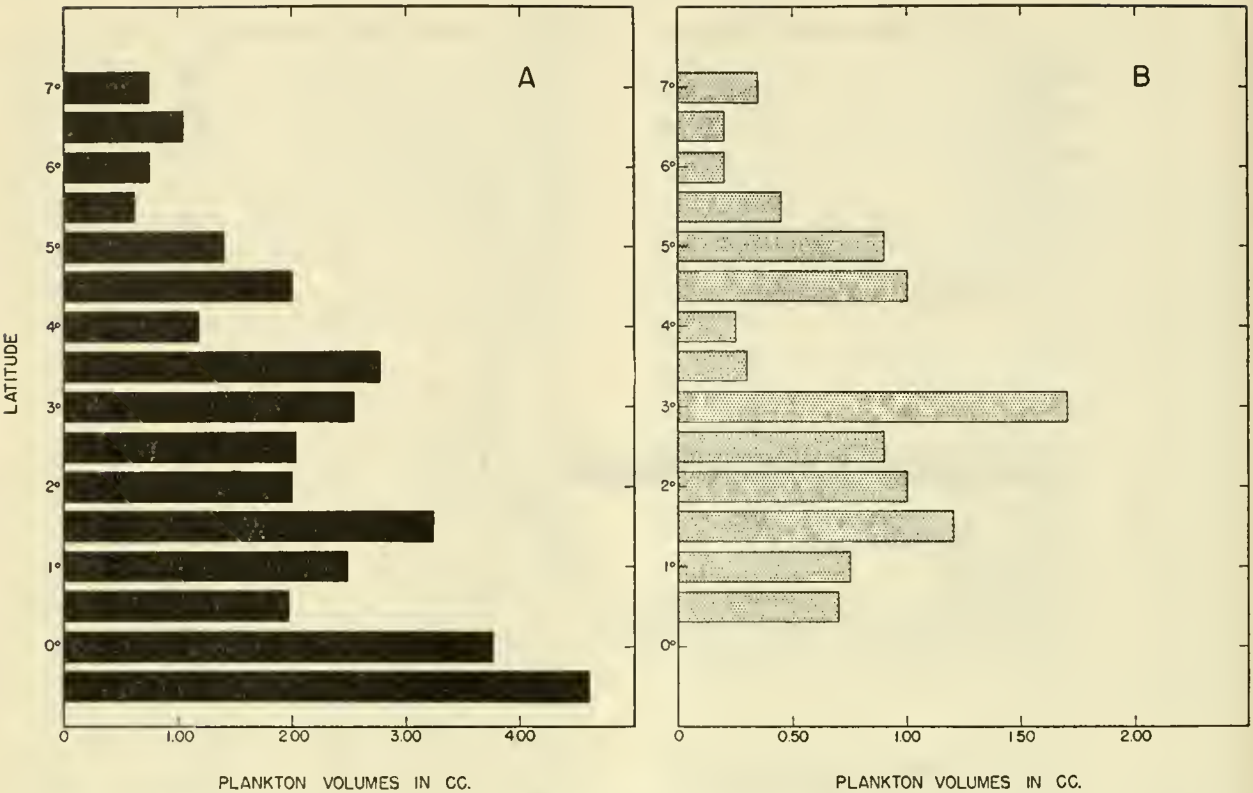

FIGURE 11.—Plankton abundance in the western Pacific: Results given are settlement volumes of total (?) plankton obtained by vertical hauls at 50 to 0 meters along 134° E. longitude. A. As reported by Tokioka (1942) for three cruises, December 1939, March 1940, and May 1940 (averaged by the senior author). B. As reported by Haneda (1942) for one cruise, December 1939.

(1935), summarizes the results as follows (the volumes expressed are catches per 1-hour haul using 1½-meter stramin nets with 50 and 100 meters of wire out):

> A notable fact here is, that we find specially large volumes in the eastern part of the Pacific, from the Bay of Panama to the Marquesas Is., with a distinct maximum (1,125 cc.) at St. 2,558, which lies west of the Galapagos. On the stretch from the Marquesas to Tahiti we have decreasing quantities of plankton (ca. 150–200 cc.), whilst on the sections from Tahiti—Cook Island (Rarotonga)—Samoa—Fiji the quantities are very small, less than 100 cc. We thus have extremely little macroplankton in this area of the central part of the Pacific, yet a series of stations just north of Samoa yielded somewhat larger quantities (ca. 100–260 cc.). From Fiji to New Caledonia also the quantity of macroplankton increases (ca. 125–210 cc.) and a further increase is shown in the section from New Caledonia down towards Kermadec Islands.

For comparison, in the North Atlantic the expedition obtained volumes ranging from 90 to 7,250 cc. per hour of hauling.

The very extensive plankton data presently being collected by the California Cooperative Sardine Research Program (California, Progress Report 1950, and unpublished data) are quite comparable to our own in most respects. Similar nets have been used by both investigations, and the results are expressed in similar units. Whereas the Sardine Research Program employed an oblique tow to a depth of 70 meters for the collections reported here, our oblique tow descended to 200 meters. This difference in sampling method probably had no great influence on the difference in results obtained. If we consider 22 of their farthest offshore stations, located between 25° N. and 33° N. latitude and visited in September 1950, we find that the average for the group was 0.057 cc./m.^{3}, which is approximately equivalent to our average (table 11) for the South Equatorial Current near the Equator but 3 times the average for the North Equatorial Current. Values for regions of upwelling close in to the California coast were as high as 14.595 cc./m.^{3} in February 1950. This is many times our maximum value of 0.1025 cc./m.^{3} The average of 0.208 cc./m.^{3} for the entire West Coast between 25° N. and 47° N. in April and May 1949, is just about 10 times our mean for the central equatorial Pacific.

Other regions of sparse plankton are found in the Gulf Stream and in the Sargasso Sea of the Atlantic Ocean. These areas apparently have much poorer plankton populations than Atlantic coastal and continental shelf waters (Clarke 1940; Riley 1939b; Riley and Gorgy 1948).

Table 18 is a summary of representative plankton values for various areas of the Atlantic and Pacific Oceans. Part of the variation in these values may be due to differences in mesh size among the nets used by different investigators. The averages for the central Pacific are the poorest of the lot; in fact they are so low that one is inclined to speculate as to how the pelagic fish populations, particularly the relatively large population of tunas, are supported.

TABLE 18.—*Comparison of plankton abundance in various areas of the Atlantic and Pacific Oceans*

[Values given in wet volume, estimated number, or wet weight]

Area	Plankton values	Mesh aperture of net used	Reference
PACIFIC AREA:			
Samoa to the Marshalls via the Equator	0.4 to 0.95 cc./m.^{3}	0.33 mm	Kramer (1906).
Java Sea	Avg.=0.83 cc./m.^{3}	0.33 mm	Delsman (1939).
Open sea, Palau Is.	110 to 530, no./m.^{3}	0.33 mm	Motoda (1940).
Bikini, just outside reef	26.23 to 62.20 no./m.^{3}	0.37 mm	Johnson (1949).
West coast, U. S. (offshore stations)	0.016 to 0.129 cc./m.^{3} Avg.=0.057 cc./m.^{3}	0.65 mm	California prog. rept. (1950).
Central Pacific	5 to 109, no./m.^{3} Avg.=35 0.002 to 0.102 cc./m.^{3} Avg.=0.027 cc./m.^{3}	0.65 mm	This report.
ATLANTIC AREA:			
Baltic Sea	1.9 to 11.0 cc./m.^{3}	0.33 mm	Kramer (1906).
Gulf of Maine (10 to 100 m. depth)	0.12 to 4.30 cc./m.^{3}	1.25 mm., front; 0.8 mm., middle and rear	Bigelow (1926).
North Atlantic (coastal water)	Avg.=0.5 to 0.8 cc./m.^{3}	29.38 meshes/in., front; 48.54 meshes/in., rear	Bigelow and Sears (1939).
Florida Strait	0.02 cc./m.^{3}	0.158 mm.	Riley (1939b).
Gulf Stream, off Florida	0.05 cc./m.^{3}		
Gulf Stream, off Georgia	0.07 cc./m.^{3}		
North Atlantic continental slope	4.3 cc./m.^{3}		
North Atlantic, coastal	8.1 cc./m.^{3}		
North Atlantic, coastal	Avg.=0.54 cc./m.^{3} Max.=15.5 cc./m.^{3}	10 strands/cm	Clark (1940).
North Atlantic, offshore	Avg.=0.40 cc./m.^{3} Max.=3.5 cc./m.^{3}		
Sargasso Sea	Avg.=0.045 gm./m.^{3}	0.158 mm	Riley and Gorgy (1948).
Gulf Stream	1 sta.=0.137 gm./m.^{3}		
Slope water	2 sta.=0.14 and 1.6 gm./m.^{3}		

PRODUCTIVITY

The practical application of most plankton research is to provide data for estimating and comparing the productivity, or available food, in various areas of the sea. It has been strongly emphasized in more recent plankton literature that the "standing crop" does not give a true measure of the rate of production. Harvey (1934) and Harvey et al. (1935) have shown that the size of the standing crop of phytoplankton is greatly affected by the grazing of animal herbivores and therefore at any one time is merely a momentary balance between the processes of production and consumption. In the tropics, steady grazing by predators may keep the zooplankton at a lower level of abundance than in higher latitudes where seasonal features of the environment allow the plankton to "pulse" or bloom and thus increase much faster than the predators. The apparently low standing crop may be considerably counterbalanced by a high rate of turnover and nearly uniform production throughout the year.

It is generally assumed that in water masses where the annual plant production is great the density of the animal population will also be great. This assumption is roughly borne out by general observations (Harvey 1945). Delsman (1939) has stated, "Where no rich plankton can develop, no rich macrofauna, no abundant fish population can either be expected." In the same vein, "The dependence of various elements of the food chain on a preceding one, conditions the distribution of the larger forms" (Hesse, Allee, and Schmidt 1951). Also, it is reasonable to believe that the zooplankton population will be the maximum that the plant crop can support. Local situations may not conform to this generality, but when large areas are considered, there is usually found a direct relation between concentrations of phytoplankton and zooplankton (Riley and Bumpus 1946). In conducting a fish-farming experiment, Raymont (1947) found that in both enclosed and unenclosed small sea areas the addition of a nitrate and phosphate fertilizer stimulated phytoplankton growth, which in turn maintained a high density of zooplankton which promoted a rapid growth of flatfish.

From tuna-catch records and observations on occurrence of surface schools, the Pacific Oceanic Fishery Investigations is accumulating evidence on the distribution of tunas which indicates quite definitely that areas of the greatest zooplankton abundance in the central Pacific are also areas of greatest tuna abundance.

We are fully aware that the data we have presented on the variation of zooplankton abundance with latitude does not in any way reflect the "rate of turnover," the most difficult element to determine in estimates of productivity. In this area of the tropical Pacific, with temperatures very uniform in time and space and zooplankton very uniform in composition, the rate of turnover should not be a disturbing feature in the comparison of the several parts of our area, i. e., for our data standing crop should be proportional to productivity.

SUMMARY AND CONCLUSIONS

1. This report presents the results of 210 quantitative zooplankton collections made in the central Pacific in 1950 and 1951, between 27° N. and 14° S. latitude, and 155° and 175° W. longitude.

2. Most of the collections were obtained by oblique hauls to 200 meters' depth, employing 1-meter nets of 30xxx grit gauze with aperture widths of 0.65 mm.

3. A method of sampling was developed that harmonized with hydrographic and fishing operations, required little of ship's time, and involved no particularly elaborate treatment of samples in the laboratory.

4. The zooplankton taken by our collecting method was composed on the average by number, of 57 percent Copepoda, with the other chief components ranking as follows: Chaetognatha, 12 percent; Tunicata, 6 percent; Euphausiacea, 5 percent; Siphonophora, 4 percent; and Foraminifera, 4 percent.

5. The composition of the collections was remarkably uniform when longitudes and cruises were compared.

6. Despite the use of oblique tows to 200 meters' depth, we found significant differences between day hauls and night hauls.

7. Since distinctly larger catches were obtained on the "summer" cruise (cruise 5) than on the "winter" cruise (cruise 8), a seasonal difference in zooplankton abundance is indicated.

8. Within the range of latitudes sampled, the greatest abundance, both by number and volume, of zooplankton occurred in the region of the Equator; sometimes the greatest concentrations were found north of the Equator, when related to a convergence, and to the south when no marked convergence existed.

9. The abundance of zooplankton is correlated with such chemical and physical environmental factors as inorganic phosphate, water temperature, dissolved oxygen, and thermocline depth, which are influenced by the upwelling resulting from the equatorial divergence.

10. Upwelling along the Equator replenishes the supply of nutrients in the euphotic zone, thus providing a favorable environment for the growth of phytoplankton. Since animal life fluctuates with its food supply, conditions in this region are favorable for the development of a zooplankton population.

11. While our observations on the standing crop of zooplankton do not give a measure of the rate of production in its strict sense, we believe that they do provide a useful index to the relative productivity of different areas of the central Pacific.

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NATURE OF VARIABILITY IN TRAWL CATCHES

BY CLYDE C. TAYLOR

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NATURE OF VARIABILITY IN TRAWL CATCHES

By CLYDE C. TAYLOR, *Fishery Research Biologist*

A fundamental problem in deriving the characteristics of a population from a series of samples is the determination of the magnitude and sources of variability in successive samples. Such variability may arise (1) from the manner in which the population is distributed in space and (2) from variations inherent in the method selected for sampling. This paper considers the variability associated with catches of fish by the otter trawl with respect to such sources. Aspects of this problem have been considered by Thompson (1928), Hickling (1933), and Barnes and Bagenal (1951). Parallel problems for plankton have been treated by Winsor and Walford (1936), Winsor and Clarke (1940), Silliman (1946), and Barnes (1949a, 1949b, 1951).

Winsor and Walford considered that "the variation actually observed in plankton sampling is the result of (a) variations in the distribution of the organisms and (b) variations in the mode of sampling. Under (b) are included such factors as variations in the speed of hauling, deviations of the haul from the vertical, completeness of washing the net, etc." It is obvious that similar factors under (a) and (b) would affect the variability of trawl hauls.

Since the chi-square distribution of paired plankton hauls did not satisfy that expected for a Poisson distribution of the organisms, Winsor and Walford examined the variability arising from factors under (b) and concluded that "a limit to the precision of estimate is set by the relative variability of the volume sampled."

Silliman (1946) studied the variability in plankton-tow-net catches of Pacific pilchard eggs. He concluded that "most of the variability of egg counts is due to real differences in egg concentration."

Barnes (1949a) studied the variability in paired plankton hauls. Following a treatment of the data parallel to that of Winsor and Clarke, he concluded that his results "are not at variance with the suggestion that the animals are randomly distributed, and that the variations observed are largely dependent upon variation in the volume of water filtered by the net."

Barnes (1949b) proceeded to examine the variability arising from variations in the volume of water sampled, by comparing the catches of plankton organisms taken by pump samples in which the volumes of water actually sampled could be determined with considerable accuracy. Barnes found that the variability associated with pump samples was no less than that with net samples and that the distribution of chi-square was similar to that found by Winsor and Walford (1936). Barnes' contribution indicates clearly the necessity for reexamining the assumptions concerning the distribution of the organisms in space.[1]

SAMPLING PROCEDURE

A census of fish populations on Georges Bank (Area XXII, subareas G, H, J, M, N, and O, fig. 1), using the research vessel *Albatross III*, was completed for the summers of 1948, 1949, and 1950. A stratified random selection of stations was designed to sample uniformly the depth zones of the bank from 10 to 200 fathoms. At each station a standard half-hour tow was made using a modified No. 1½ Iceland trawl with belly and cod-end liners of 1½-inch-stretch cotton mesh in order to catch fish as small as possible. At each trawl station, all fish were counted, representative samples were measured, and temperature data from surface to bottom were obtained by the bathythermograph. A second tow was made at randomly selected stations in 1948 and at every third station in 1949 and 1950.

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[1] Assuming a heterogeneous distribution of plankton organisms, Barnes has shown in a recent study that the distribution of plankton-tow-net catches conforms satisfactorily to the "contagious" distribution of Thomas (1949). See Barnes (1951).

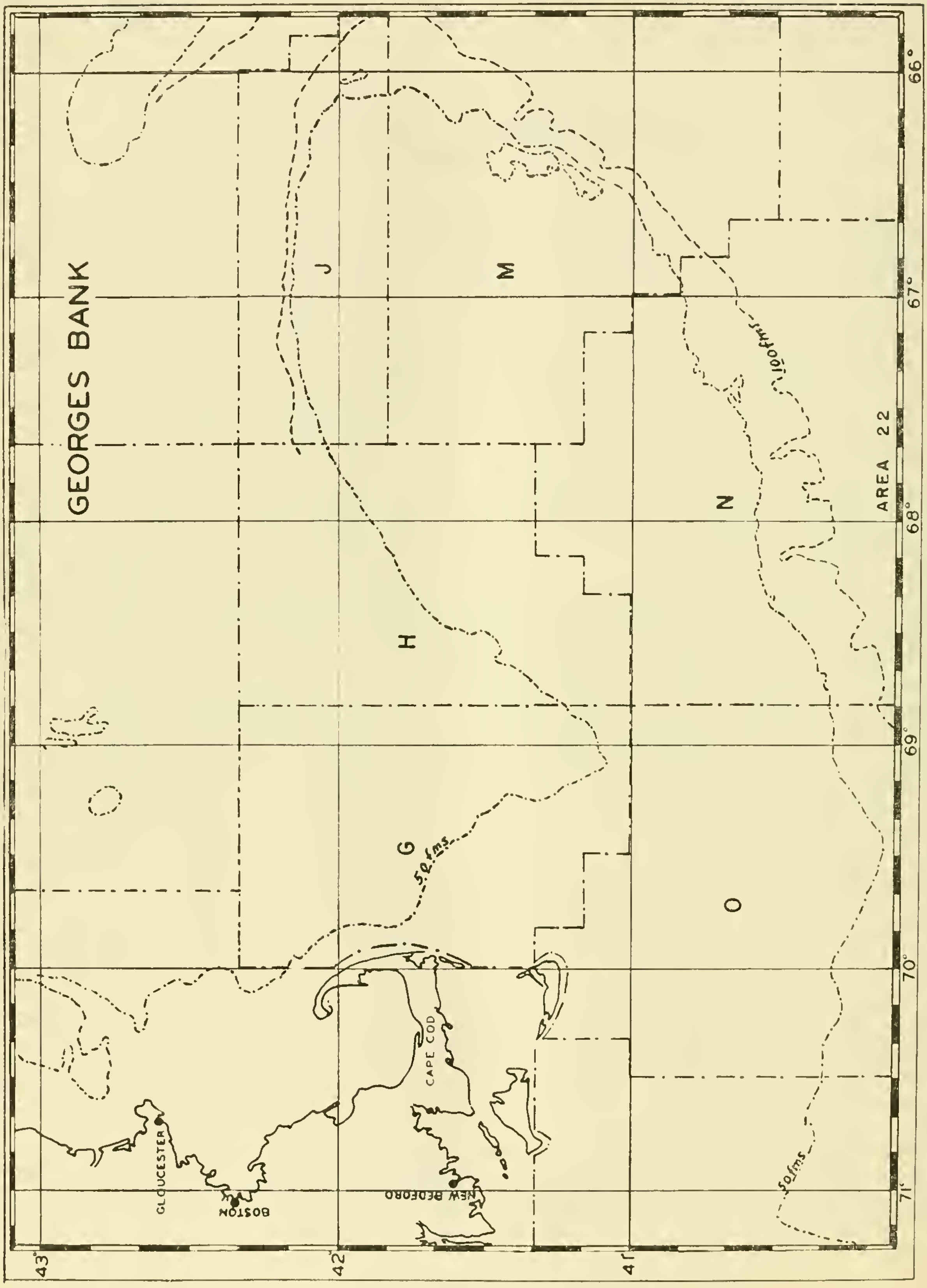

FIGURE 1.—The statistical subareas of Georges Bank.

TWO-TOW STATION DATA

Since two tows were made at approximately one-third of the stations in 1948, 1949, and 1950, the series of paired observations furnishes a measure of comparative variability between tows.

As Winsor and Walford (1936) show, if the basic distribution is Poisson the quantity

$$\chi^2=\sum\frac{(n-\bar{n})^2}{\bar{n}^2}=\frac{(n_1-n_2)^2}{n_1+n_2}$$

should, in a number of random samples, have a mean value of 1 and should be distributed in a known manner.

Table 1 shows the distribution of values of chi-square for haddock, whiting, and the common skate, and for total fish. The distribution is of the same type as those found by Winsor and Walford (1936) and Barnes (1949a) for plankton, with an excess of large values of chi-square.

In table 2, the totals of chi-square are classified by sample size. Although there is some tendency for the larger hauls to be associated with high chi-square values, the values are generally high for all levels of catch. While variability in sampling is expected to arise from imperfections associated with the sampling technique, it is clear that if the data are taken from a population distributed at random these imperfections would have to be of the grossest kind to account for the variability observed.

As a working hypothesis, the assumption of a random distribution of plankton organisms does not appear unreasonable, even though such an assumption seems to have been suspect for some time. A similar assumption for the distribution of fish, however, appears quite unwarranted, since trawl catches, fathometer records, and the observations and experience of fishermen indicate that fish tend to congregate in schools. Trawl catches show that these schools are heterogeneous and that, while a particular species may predominate, there is ordinarily a variety of species represented. These schools probably differ not only in area but also in density within an area.

In table 3, the catches of haddock in tow 1, tow 2, and tows 1 and 2 combined are tabulated for the two-tow stations. It is at once apparent that the observed curve of distribution cannot possibly be Poisson unless the mean is less than 1, which it obviously is not.

The observed distribution of frequencies of catch per tow of haddock suggests the negative binomial distribution (Greenwood and Yule 1920). The combined data for the two-tow stations (table 3) were therefore fitted by the negative-binomial distribution.[2] Details concerning the goodness of fit are summarized in table 4.

This development suggested that the basic distribution of the catch-per-tow data might be the negative binomial. It became necessary to examine not only the validity of this hypothesis in the light of the data at hand but also any theoretical reasons why these data should be so distributed.

Negative binomial series were fitted to catches of haddock per standard tow for each of three depth zones: Depth zone 1, 0–30 fathoms; depth zone II, 30–60 fathoms; and depth zone III, more than 60 fathoms. While no particular significance is thought to attach to these groupings, the data were available in these classifications, and these depth zones are presumed to represent a certain homogeneity of conditions. The results of these fittings are presented in table 5. The catches for depth zone III are presented in figure 2.

Similar treatment was accorded the data for the common skate (*Raja erinacea*), the whiting (*Merluccius bilinearis*), and the ocean perch (*Sebastes marinus*). These data are presented in tables 6, 7, and 8. The catches for common skate and ocean perch are presented in figures 3 and 4.

The probabilities associated with the $\Sigma\chi^2$ for these data are summarized in table 9. They are sufficiently high to retain the hypothesis that the basic distribution is the negative binomial. This hypothesis is strengthened, however, if theoretical grounds, conforming to conditions known to apply to the data, may be found.

Let us first consider a Poisson distribution with mean m.[3] Two essential conditions for a Poisson distribution of items are that they be distributed at random and independently of one another. If the items are not distributed independently but tend to cluster in groups,[4] the estimate of m will tend to vary with sampling, and a Poisson distribution will no longer be obtained.

---

[2] See appendix B.

[3] The development follows in its essentials that demonstrated by Fisher (1941).

[4] Compare the "contagious" distributions of Polya, 1931; Neyman, 1939; Cole, 1946; and Thomas, 1949.

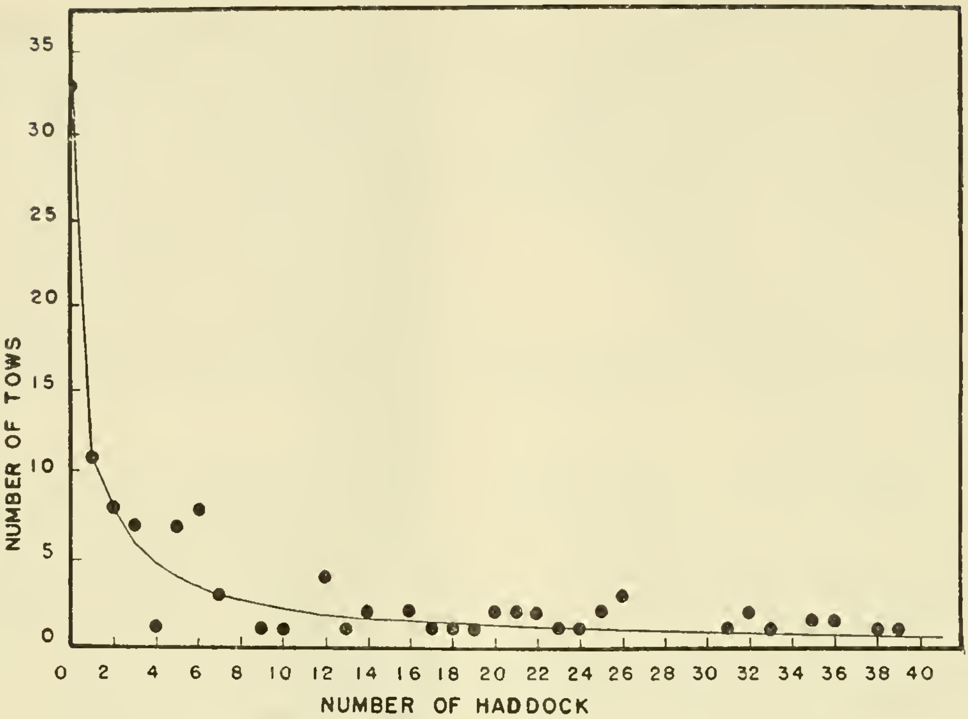

FIGURE 2.—Number of tows, number of haddock, and the fitted binomial distribution.

Fisher (1941) considered the simplest frequency distribution which allows for some variation of m to be the Eulerian distribution with frequency element:

$$df=\frac{1}{(k-1)!}p^{-k}m^{k-1}e^{-m/p}dm \quad \ldots\ldots(1)$$

When m varies in this way, the frequency of occurrence of x units in the sample is:

$$\int_0^\infty \frac{1}{(k-1)!}p^k m^{k-1}e^{-m/p}e^{-m}\frac{m^x}{x!}dm \quad \ldots(2)$$

leading to the integral of the Eulerian type:

$$\frac{(k+x-1)!}{x!(k-1)!}\cdot\frac{p^x}{(1+p)^{k+x}} \quad \ldots\ldots\ldots(3)$$

which is identical with the standard form of the negative binomial.

In the derivation of the negative binomial distribution, it is important to consider that while the Poisson distribution is that expected for homogeneous material, the Poisson no longer holds if (1) there is variation in the size of the samples or (2) if the material is heterogeneous. The variation (in excess of that expected for a Poisson distribution) observed in plankton and trawl sampling has been attributed in the past to factors falling under (1), e. g., variations in the volume of water sampled. It is clear that variability may be ascribed equally to heterogeneity in the population sampled, i. e., "true" sampling variation. This heterogeneity, furthermore, does not exclude the possibility of a stable [5] mathematical distribution amenable to statistical treatment.

DISTRIBUTION OF SPECIES AND NUMBERS OF FISH

The number of fish of each species was recorded for each tow made over the period 1948–50. The logarithmic series having been developed by R. A. Fisher (1943) to account for peculiarities in the distribution of species and numbers of individuals of each, it appeared desirable to determine whether the species occurring in the trawl samples were so distributed.

---

[5] By "stable" we mean a distribution whose general characteristics do not change between successive sets of samples. Heterogeneity, while a condition for a negative binomial distribution, does not necessarily imply the negative binomial distribution as the only possibility.

The trawl-catch data were classified by the same depth zones as were used above. The number of species, S, and the number of individuals, N, were determined for each depth zone in each year, and also for each depth zone for the 3 years combined, 1948–50. Logarithmic series were fitted to each grouping. Goodness of fit was determined in the usual way. The data were grouped so that the number of expected observations was close to five. After the first few terms, the interval of grouping necessary to obtain five expected observations increases rapidly so that in general it is not feasible, or necessary, to compute the series beyond the first four or five groupings, these groupings usually including the first 150 to 200 terms.

The results of fitting logarithmic series to the distribution of species and numbers of fish represented by each are presented in tables 12 (a, b, and c) and 13 (a, b, and c), together with the chi-square for each grouping and the probability of obtaining a worse fit by chance for the total chi-square. It is apparent that the hypothesis of logarithmic distribution cannot be rejected.[6]

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[6] The relationship of the logarithmic series to the negative binomial is discussed (p. 155 and appendix A). Derivation of the logarithmic series and some of its mathematical properties are presented in appendix C.

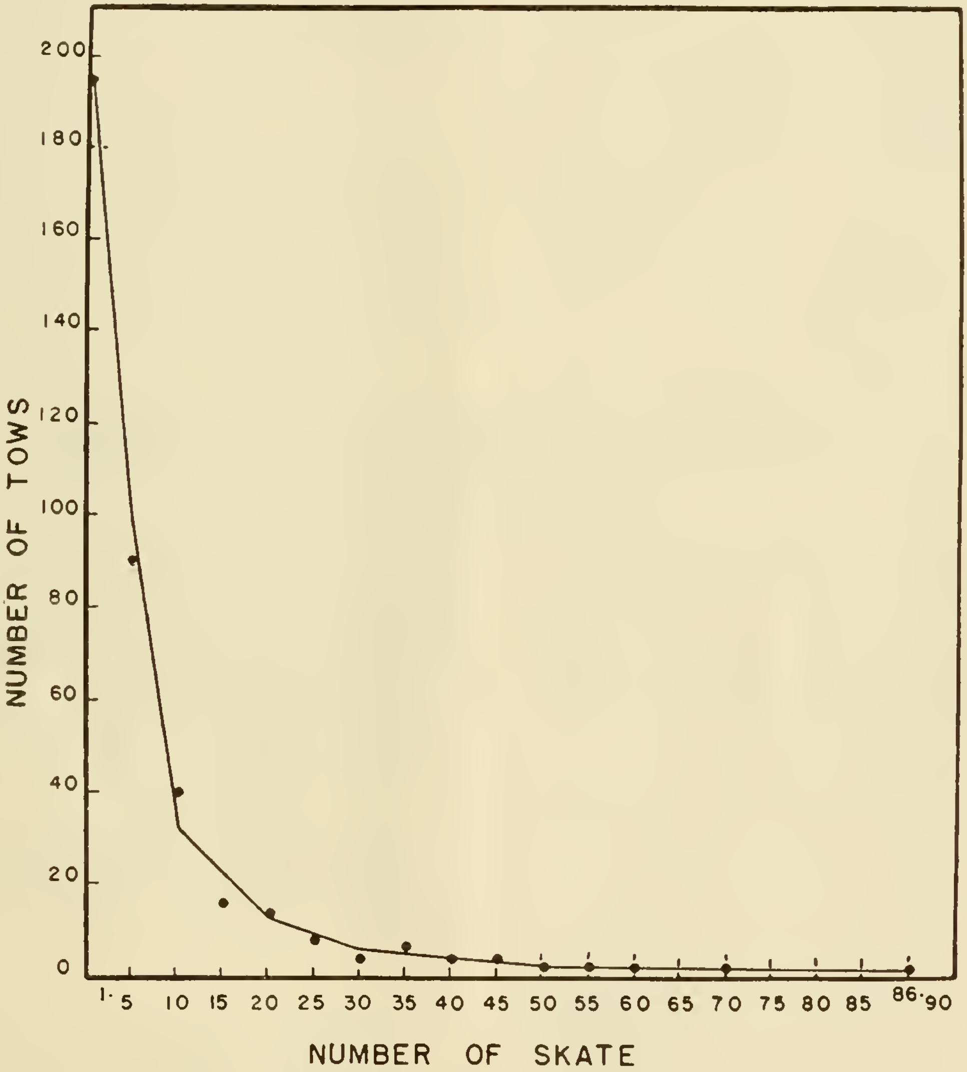

FIGURE 3.—Number of tows, number of common skate, and the fitted binomial distribution.

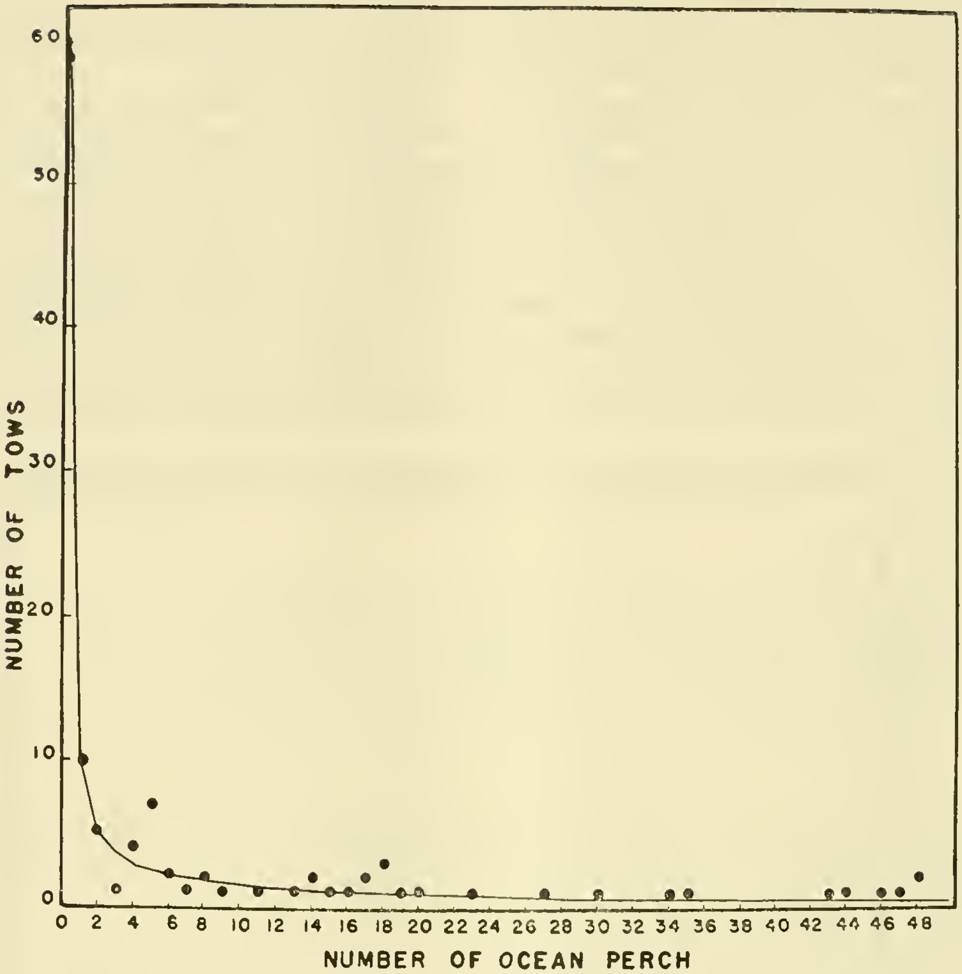

FIGURE 4.—Number of tows, number of ocean perch, and the fitted binomial distribution.

Williams (Fisher, Corbett, and Williams, 1943) has suggested that the index α of the logarithmic series be called the "index of diversity," since it is a measure of the richness in species from sample to sample. Williams (1944) has given a summary of the properties of the index of diversity, which (slightly condensed) is as follows:

(1) If several samples are taken from the same population, not only will they have the same index of diversity, but when two or more of them are added together the combined sample will still have the same index.

(2) Different populations may have, by chance, the same index of diversity, and samples from them will have the same index. When these samples are added together, however, the alpha of the combined sample will be larger than that of either of the two or more original samples.

(3) If two populations are entirely apart, then the index of one sample from each combined will be the sum of the two indices for each sample separately. If there is some overlap, alpha will be larger than either but smaller than the combined total.

(4) If two samples, not of very small size, are taken from the same population, the larger sample being p times the smaller, then the number of species in the larger sample will be $\alpha \log_e p$ more than in the smaller; it follows that the index α is the number of species added to a sample by multiplying its size by e.

(5) In the same population, x approaches 1.0 as the size of the sample increases, and n_1 approaches α (where n_1 is the number of singleton species).

From these properties of the index of diversity, it is apparent that a useful analytical device is provided for examining the characteristics of populations, provided the logarithmic distribution is applicable.

SOME APPLICATIONS OF THE LOGARITHMIC SERIES TO THE TRAWL DATA

The trawl data collected from 1948 to 1950 on Georges Bank were classified by depth zone and bottom type, and the index of diversity and its variance[7] were calculated for each classification. The data for depth zones are presented in tables 15a and 15b. Direct comparisons of pairs of values of the indices were made considering differences greater than twice the standard error of their difference to be significant. Since many comparisons are possible, one must remember that about 1 in 20 of such comparisons may be significant at the 5-percent level.

None of within-year and between-year comparisons of indices of diversity by depth zones were significant, so that one may conclude that in "richness of species" the depth zones do not differ significantly either within or between years. This does not mean that the species composition does not vary with depth zone but rather that the relation of the variety of species to the total number of fish in each depth zone and in each year is about the same.

A measure of the differences in species composition which exist among depth zones may be obtained by combining data for the various depth zones under consideration. If no differences exist, the resulting index will be about the same as those for the depth zones from which the combined sample was taken. If the depth zones differ completely in species composition, the resulting index will be the sum of the individual indices. The depth-zone data combined in this way show increases in the indices of diversity, but they are rather small (table 14). It is evident that there must be many species common to all depth zones with fewer species restricted to one alone. This is borne out by the observed depth distribution of the various species.[8]

Bottom samples were attempted at each station where trawls were made. These data were compared with and supplemented by data from Coast and Geodetic charts and classified into four general types: sand, mud, mud and sand, and stony. Indices of diversity were calculated for each bottom type in each depth zone for each year and also for the three years combined. The indices were compared in the usual way, the difference being divided by the standard error of the difference.

Only one difference significant at the 5-percent level was found. Since 30 comparisons were made, we may expect at least one significant difference to appear by chance. These tests do not, then, reveal any evidence of significant differences in the diversity of species either between bottom types within depth zones, or between depth zones within bottom types.[9]

DISTRIBUTION OF SPECIES PER TOW

In the logarithmic series, the distribution of the number of species, S, is Poisson (Anscombe 1950). We may, therefore, further examine the trawl data to find whether the observed distribution of species per tow conforms with theory.

In table 15 the number of species per tow and the number of tows are presented for the years 1948–51. The data for all tows in the Georges Bank area are tabulated in column A. In column B, the first three tows of each cruise and the first three tows following a change from the port to starboard trawl net, or vice versa, have been eliminated.

Data for 1949a and 1950a may be fitted with Poisson distributions with probabilities somewhat greater than 0.10 and 0.80, respectively. The data 1948a and 1951a are fitted with probabilities so low that the hypothesis of a Poisson distribution must be rejected.

Data for 1949b, 1950b, and 1951b are fitted with Poisson distributions with probabilities greater than 0.30, 0.80, and 0.30, respectively. Data for 1948b does not give a satisfactory fit. The observed and expected values are presented in table 16, together with $\Sigma\chi^2$ ($n-2$ degrees of freedom).

There is no reason to reject the hypothesis that the distribution of number of species per tow is Poisson. It is apparent from table 16 that factors are operating in the sampling procedure which tend to result in tows with a small observed number of species. The greatest number of these tows occur in 1948 and 1951; 1948 was the first year of the census sampling. In 1951 a different vessel, the *Delaware*, was used. One is inclined, then, to suspect that factors affecting the efficiency of operation of the trawl net are the cause of a large number of tows containing a small number of species in these years.

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[7] See appendix C for the formula used in calculating the variance.

[8] The statistical significance of the increase in the index through combining cannot be determined by comparing the difference with the standard error of the difference, since the variates compared are no longer independent.

[9] Preliminary analyses of variance of the transformed catch-per-tow data indicate consistent significant differences in the distribution of particular species by bottom type. The distribution of species by bottom type may be studied by analysis of variance or by χ^2-contingency tables, after a square-root transformation of the number of species per tow.

The improvement in agreement of the observations with hypothesis which occurs when the first three tows are eliminated suggests that a dry net does not fish efficiently. This may be true but, on the other hand, the elimination of these tows in the 1950 data makes practically no change at all in the species-per-tow distribution. The trawl data are being studied in an effort to find an adequate explanation of the departure of species-per-tow distribution from theory.

It is evident that if we accept the hypothesis of a Poisson distribution of species per tow, we have a useful method of gauging the efficiency of the sampling procedure. The data presented in tables 15 and 16 suggest that tows are present in the data which ought to be rejected for purposes of further analysis, provided an objective basis for their rejection can be discovered. A Poisson distribution of the occurrence of species in tows also provides means for further study of differences between bottom types, depth zones, or other environmental factors.

USE OF CATCH DATA IN THE ANALYSIS OF VARIANCE

When the program for sampling fish populations on the fishing grounds was planned it was anticipated that the technique of analysis of variance could be applied to extract as much information as possible from the body of data to be collected, and the sampling program was designed with this technique in mind. A necessary condition, however, for a valid analysis of variance is that there be a constant residual variance. If the variance changes with the mean level, a suitable transformation is necessary to stabilize the variance.

If the variance can be expressed as a function of the mean m, it has been shown (Curtis 1943) that the appropriate transformation may be determined.

In the early stages of the present analysis, it was found that the standard deviation of the catches per tow was approximately proportional to the mean for many species. Typical examples are presented in tables 10 and 11 and figures 5 and 6 for haddock and whiting catches. The relation between the standard deviation and the mean may be expressed

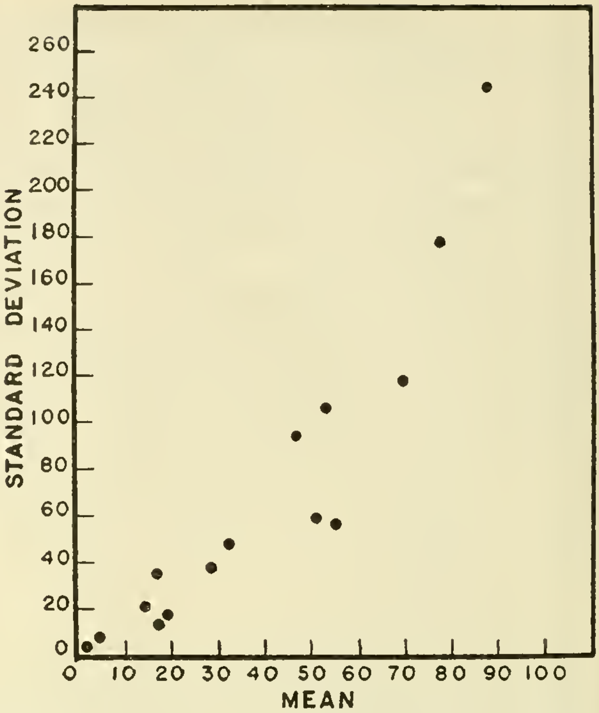

FIGURE 5.—The mean and standard deviation of haddock catches for the subareas and depth zones of Georges Bank.

$$\sigma_x = km \qquad (4)$$

where σ_x is the standard deviation of catches x with the mean of x equal to m.

It is shown by Bartlett (1947) that for any function $g(x)$, we have approximately

$$\sigma_g^2 = (dg/dm)^2 f(m) \qquad (5)$$

so that if σ_g^2 is to be constant, K^2 say, we must have

$$g(m) = \int \frac{K dm}{\sqrt{f(m)}} \qquad (6)$$

From equations 4 and 6 we have:

$$f(m) = \sigma_x^2 = k^2 m^2$$

and

$$g(m) = \int \frac{K dm}{\sqrt{k^2 m^2}}$$

or

$$g(m) = (K/k) \log m + C \qquad (7)$$

where C is a constant introduced by integration.

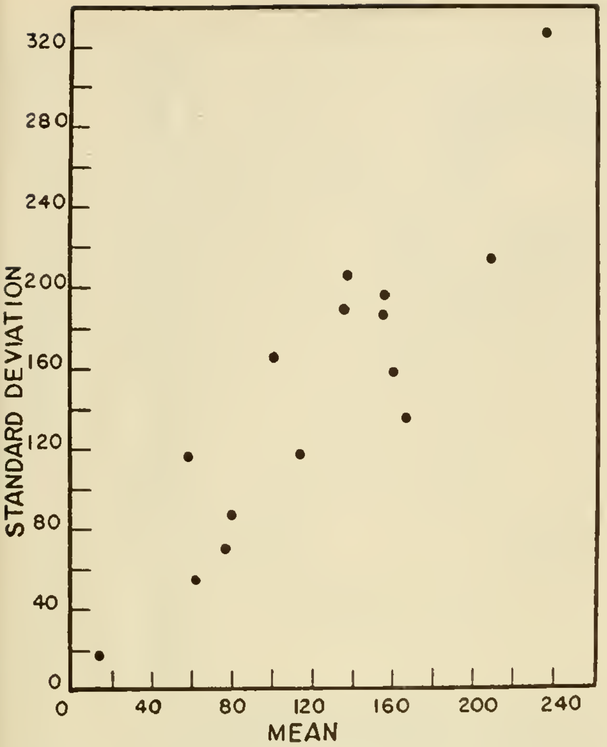

FIGURE 6.—The mean and standard deviation of whiting catches for the subareas and depth zones of Georges Bank.

Equation 7 indicates a logarithmic transformation of the catch data. This transformation has been frequently employed in the past in the treatment of both plankton and trawl data (Winsor and Clarke 1940; Silliman 1946; Barnes, 1949a, 1949b, 1951).

It has been demonstrated above, however, that the hypothesis of a negative binomial distribution graduates the trawl data satisfactorily. The relation between the mean and variance for a negative binomial distribution is

$$\sigma_x^2 = m + m^2/k \ldots\ldots\ldots\ldots\ldots (8)$$

Applying equation 6 we have

$$g(m) = \int \frac{K dm}{\sqrt{m + m^2/k}}$$

leading to either a $\sinh^{-1}$ or logarithmic integral. Anscombe (1948) shows that for a negative binomial distribution with variable x, exponent k, and mean m, the appropriate forms of the transformation are

$$y = \sinh^{-1}\sqrt{\left(\frac{x+C}{k-2C}\right)} \ldots\ldots\ldots\ldots (9)$$

and $$y = \log\,(x + \tfrac{1}{2}k). \ldots\ldots\ldots\ldots (10)$$

If m is large and k greater than 2, the optimum value of C (equation 9) is roughly $\frac{3}{8}$. With k less than 2 but greater than $\frac{3}{4}$, and m large, the simpler transformation (10) may be used.

The negative binomial distributions which have been fitted to the catch-per-tow data have, generally, a fairly large m, but the value of k is, in all instances, less than $\frac{3}{4}$. Under these circumstances, it is apparent that the difference between the transformations indicated by equations 7 and 10 is slight. In applying equation 7, it is customary to use the empirical transformation log $(1+x)$ to avoid difficulty with zero observations. Equation 10 has the advantage of assigning a numerical value to zero observations, based on properties of the observations themselves and may be preferable in some cases.

DISCUSSION

The distribution theory

It has been shown that the distribution of catch per tow for various species of fish caught by the research vessel *Albatross III* over a 3-year period on Georges Bank conforms to the negative binomial distribution. On the other hand, the distribution of species and numbers of individuals represented by each conforms satisfactorily to Fisher's logarithmic series distribution.

Anscombe (1950) lists seven 2-parameter distributions constructed on models postulating various types of heterogeneous Poisson sampling. Considering only the catch-per-tow data, there appear to be three of these distributions, in addition to the negative binomial, which might be applied: the Neyman Type A, the Polya-Aeppli, and the Thomas, all three being of the so-called contagious type. These distributions are examined, since the trawl catches may represent samples from populations so distributed. The three distributions are similar in supposing a Poisson distribution of colonies or groups, but they differ in the assumptions concerning the distribution of items within groups. In the Neyman

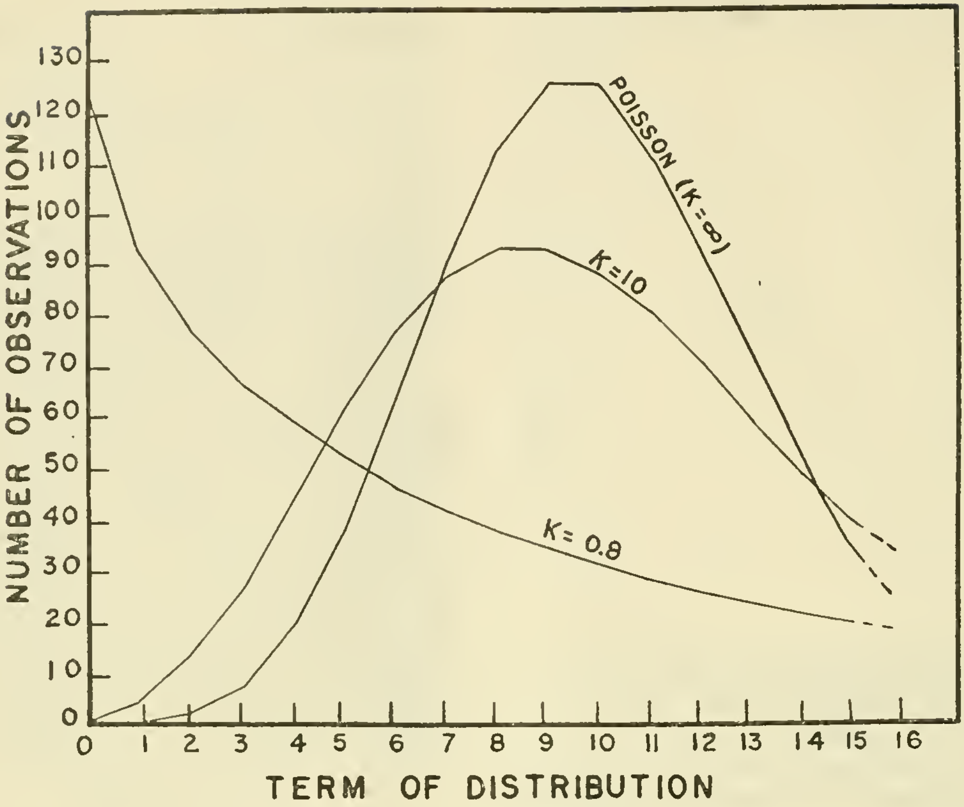

Figure 7.—The negative binomial distributions compared to the limiting form, the Poisson. Each distribution has a mean of 10 and consists of 1,000 observations.

Type A distribution, the number of colonies or groups per sample has a Poisson distribution with mean m_1, while the number of individuals per group has a Poisson distribution with mean m_2. The Thomas distribution is similar, the number of individuals per group assumed to be one plus an observation from a Poisson distribution with mean m_2. The Polya-Aeppli distribution, however, supposes that the number of individuals per colony has a geometric distribution; it has, therefore, some interest in connection with sampling from growing populations (Anscombe 1950).

In the absence of a series of equally spaced modes, Anscombe (1950) points out, one may reasonably feel reluctant to use the Neyman or Thomas distributions. Such modes are not evident in the trawl data.

The choice between the negative binomial and the Polya-Aeppli distributions lies less in consideration of the goodness of fit obtained in applying them than in the various theoretical considerations which might justify their use. Kendall (1948) shows that colonies established simultaneously from single ancestors and unaffected by immigration will, after a fixed lapse of time, have a distribution of population sizes resulting from growth at geometric rates equivalent to the difference between constant reproduction and mortality rates. This is the model for the Polya-Aeppli distribution provided that the distribution of the ancestors establishing each colony was random. If, on the other hand, the distribution of ancestors does not occur simultaneously throughout the area of observation but is uniform in time, the distribution of colony sizes resulting will be that of the negative binomial, provided that reproduction and mortality rates are constant. Kendall's analysis indicates that the index of the resulting negative binomial, *k*, is intrinsically associated with the reproductive power of the species.

These models for the Polya-Aeppli and the negative binomial distributions appear oversimplified in considering the application of them to fish populations. The origin of schools of fish can hardly be supposed to occur simultaneously throughout the area of observation or to arise from the progeny of a single ancestor. The condition of uniform distribution in time possibly is approximated, so that one may be inclined to favor the negative binomial as the more likely, although an essential of Kendall's model is the self-duplication of random individuals at random times.

A stronger argument in favor of the negative binomial distribution is a relation among the negative binomial, the logarithmic series, and the Poisson distributions which has been pointed out by Quenouille (1949). It is demonstrated that in sampling from a logarithmic series, the probability distribution of the number of individuals in random samples is the negative binomial. Quenouille further demonstrated that if any two of the three distributions hold, the third distribution is implied (see appendix A).

A logarithmic distribution of species and individuals is demonstrated to hold with reasonable probability for the trawl data, and it is further shown that the hypothesis of a negative binomial distribution satisfactorily conforms to the distribution of numbers per tow, as theoretically required, given a logarithmic series distribution from which samples are drawn.

The implied Poisson distribution can occur in several ways, some of which are suggested by the models considered above. The Poisson distribution of the number of species per tow suggests the hypothesis that the various species are distributed at random and move independently of one another. This hypothesis does not require that the distribution of a species be random, since a species occurs only once, no matter what its abundance in numbers, in the sample. The assumption of a Poisson distribution of species appears sufficient to complete the theory, especially when we have a certain amount of evidence that this distribution actually holds. Alternatively, we might suppose that the occurrence of schools or concentrations of fish is random. This may, in fact, be true but it cannot be demonstrated at present because of lack of the necessary observations.

Application of the distribution theory to the census problem

The problem of variance.—The primary purpose of the census cruises made on Georges Bank was to estimate and define the abundance and distribution of the fish populations inhabiting it. It is not the purpose of this paper to extend the distribution theory to numerical estimates of populations, but it is pertinent to examine certain aspects bearing on them.

In populations with individuals distributed at random and independently of each other, it is well known that the variance is equal to the mean. In a negative binomial distribution, the relation between mean and variance is

$$\sigma_x^2=m+m^2/k \quad \text{..............} (10)$$

One sees at once that the departure of the variance of the negative binomial from that of the Poisson depends on the value of k; the variance, as well as the distributions themselves, becoming identical as k tends to infinity. On the other hand, if k is less than one, the variance is never less than the square of the mean and may be of considerably greater magnitude.

The high variance associated with the mean of a negative binomial distribution introduces a most serious problem in estimation. Since k is an intrinsic property of the population being sampled, it is independent of the sampling method and its estimate is subject only to sampling variation. The mean, however, depends on the size of the sampling unit, e. g., in the census sampling, the size of the trawl net and the duration of the tow.

Taking as a measure of the precision of sampling the reciprocal of variance, the amount of information of a mean based on n observations is n/σ_x^2. It is clear that the amount of information can be increased by increasing the number of observations, by decreasing the variance, or both.

Examining the relation between mean and variance (equation 10), we see that any change in sampling method which increases the mean will increase the variance even more rapidly. It has been suggested that the trawl data could be "smoothed out" by using a smaller net and increasing the length of the tow. Increasing the length of the tow would tend to increase the mean, while decreasing the size of the net would tend to decrease the mean. If the two effects were of such magnitude as to cancel each other, the variance would, of course, remain unchanged.

On the other hand, it will be seen that changes in sampling which reduce the mean will also reduce the variance, and for a given number of observations, will increase the amount of information given about the mean. The obvious ways to reduce the mean are to reduce the length of the tow and to reduce the size of the net within practical limits.

We have, for example, in depth zone II, 171 tows in which the mean catch of haddock was 130. The value of k, calculated from the maximum-liklihood equation, is 0.25 (0.2542). The expected variance is

$$\sigma_x^2=130+\frac{130^2}{0.25}$$

or 67,730. Let us suppose that by decreasing the length of the tow and the size of the net each by one-half, we reduce the observed mean by one-fourth so that it is now 130/4 or 32. The expected variance is now $\sigma_x^2=32+32^2/0.25$ or 4,128. The amount of information has been increased by 67,730/4,128 or about 16 times. Reduction in the size of the net and the length of the tow would doubtless be accompanied by other practical advantages, such as a smaller crew to handle the net, greater ease in handling, more data on the smaller catches, and the execution of a greater number of tows within a given time period.

It is to be pointed out that, in the final analysis, we are interested in the precision of an estimate of the total population in the area sampled. The mean we observe in a series of samples with any given sampling unit is, of course, the basis for this estimate. This problem, with particular reference to a heterogeneous population, is examined in appendix E.

Ecological relations.—Since the numbers of each species occurring in the trawl catches were recorded, we have in these data, in a sense, a third dimension of observation: the relation of the species to each other and to various environmental conditions, not only in qualitative but also in quantitative terms. While some of the properties of the index α of the logarithmic series have been pointed out above, the primary purpose in the present paper has been to examine the reality of the logarithmic-series distribution of species and individuals.

Although the analysis of the indices of diversity by bottom type and depth zone within and between years does not reveal any significant differences in richness of species, an entirely different result is obtained if one uses Fisher's formula for variance (7, appendix C) rather than that given by Anscombe (8, appendix C). In our data Fisher's formula gives a variance roughly one-tenth as great as that given by the formula we have used. As a result many significant differences appear between bottom types, with an apparent tendency for these differences to diminish with depth. With Fisher's formula there still appear no significant differences between depth zones. As Anscombe points out, the conditions under which Fisher's formula is applicable are rather specialized. It is possible that closer examination of our data may reveal that some of the specialized conditions are met.

An interesting relation which may be of practical use after further study of the data is given by the formula

$$S=\alpha \log_e (1+N/\alpha) \quad \text{..........}(11)$$

When N is large compared to α, we may write

$$S=\alpha \log_e (N/\alpha) \quad \text{...........}(12)$$

Making the necessary assumption that the density of population within the total area is the same as that within the area actually sampled, we should expect to observe a total of S_t species if we sampled the entire area. Designating S_s as the number of species observed in the sample area, A_s say, the expected increase in species if we sampled the entire area, A_t, is

$$S_t-S_s=\alpha \log_e (A_t/A_s) \quad \text{.......}(13)$$

from which we can readily estimate S_t. Substituting S_t and the sample estimate of α in equation 12 we can then estimate N_t, the total number of individuals within the total area of all species. Limits of reliability of estimate may be set from the standard error of α. It is pointed out here merely that the method may be of some use when the area under consideration is not too large as compared with the area sampled, when the sampling is done within a fairly short period, and when the assumption of uniform population density can reasonably be made. Under these conditions Fisher's formula for the variance of α would be applicable.

SUMMARY

Analysis of the census-trawl data collected during three summers on Georges Bank shows that the hypothesis of random distribution of the fish of a given species is not tenable. Two theoretical distributions, developed from models postulating heterogeneity or aggregation, are shown to apply to the observed data with sufficiently high probability to retain them as working hypotheses. One of these, the negative binomial distribution, describes satisfactorily the distribution per tow of individuals of a species. The other, the logarithmic series distribution, is shown to describe the distribution of individuals and species.

The occurrence of species in successive samples is shown to have a Poisson distribution, and this, in theory, is sufficient to account for the logarithmic distribution of species and individuals observed. It is pointed out that various authors have shown that the occurrence of numbers of a particular species drawn in samples from a logarithmic distribution will be of the negative-binomial form. The observed distributions are therefore self-consistent.

A high variance associated with the mean catch per tow is shown to be a necessary consequence of the basic heterogeneous distribution of the numbers of fish. The agreement of observed variances with theoretical variances is sufficiently good to indicate that the variance due to variations in the sampling technique is of relatively minor importance.

It is shown that the variance may be reduced and the amount of information increased by decreasing the size of the observed mean, and it is suggested that this may be accomplished by reducing the length of tow and by reducing the size of the trawl net.

Appropriate transformations for use of the census-trawl data in analysis of variance and in other statistical procedures are indicated.

APPENDIX A

A model for fish population distribution

The following model is an attempt to postulate simple conditions which would lead to the mathematical distributions observed in the trawl-sampling studies. It is a restatement, in terms of species and numbers of fish, of mathematical relations which have been noted in somewhat more general terms by Fisher (1941, 1943), Kendall (1948), Quenouille (1949), and Anscombe (1950). We have borrowed freely from these authors.

Let us postulate that S species are distributed at random within the area of observation, each species moving independently of others, so that the distribution is Poisson with the probability of observing exactly n species in any one sample

$$P(n \text{ species}) = \frac{e^{-m}m^{n}}{n!} \quad \ldots\ldots\ldots\ldots (1)$$

Let us postulate further that the number of individuals represented by each species is not random but rather that the individuals of each species tend to aggregate so that the mean m varies from sample to sample in a Eulerian distribution. The probability of observing a sample of size r is, then,

$$P(r \text{ individuals}) = \frac{(k+r-1)!}{(k-1)!r!} \cdot \frac{p^{r}}{(1+p)^{k+r}} \quad \ldots (2)$$

which is the standard form of the negative binomial with index k and parameter $p/1+p=x$ (Fisher 1941; Quenouille 1949). Letting k tend to infinity and excluding the first term as unobservable, a logarithmic series distribution is obtained (Fisher 1943) where the probability of observing r individuals of one species is

$$P(r \text{ individuals of one species}) = \alpha\, x^{r}/r \ldots (3)$$

or the coefficient of t^{r} in

$$-\alpha \log_{e}(1-xt)$$

where $$x=\frac{p}{1+p} \text{ and } \alpha=-\frac{1}{\log_{e}(1-x)} \quad \ldots\ldots (4)$$

The following relations result (Quenouille 1949):

$$P\ (r \text{ individuals}) = P\ (n \text{ species}) \times P(r \text{ individuals in } n \text{ species}) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (5)$$

From equation 4 the probability of observing r individuals in n species is the coefficient of t^{r} in

$$[-\alpha \log_{e}(1-xt)]^{n}$$

Rewriting equation 5 we have

$P(r$ individuals)

$$=\text{coefficient of } t^{r} \text{ in } \sum_{n=0}^{\infty} \frac{e^{-m}m^{n}}{n!} \times [-\alpha \log_{e}(1-xt)]^{n}$$

$$=\text{coefficient of } t^{r} \text{ in } \exp\,[-m-\alpha m \log_{e}(1-xt)]$$

$$=\text{coefficient of } t^{r} \text{ in } (1-xt)^{-\alpha m}e^{-m}$$

$$=(1-x)^{\alpha m}\frac{(\alpha m+r-1)!}{(\alpha m-1)!r!}x^{r}, \text{ since } (1-x)^{-\alpha}=e. \quad (6)$$

Equation 6 is the same as the (r+1)th term in a negative binomial series with parameter x and index α m.

It is thus seen that the two basic assumptions necessary to obtain the observed distributions are (1) the species are distributed at random and move independently of one another, and (2) the individuals within each species tend to aggregate so that the mean m is a Eulerian variable from sample to sample.

APPENDIX B

Characteristics and fitting of the negative binomial distribution

The negative binomial distribution is described by two parameters, the mean m and the index k. The variance of the distribution is

$$m+m^2/k \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

The expected frequency of zeros is

$$P_0=(1+m/k)^{-k} \ldots\ldots\ldots\ldots\ldots (2)$$

and the chance of observing any positive count r is

$$P_r=\frac{k(k-1)\ \ldots\ (k-r+1)p^r}{r!}(1-p)^{k-r} \ldots (3)$$

or, more conveniently, letting $p'=-p$, $k'=-k$,

$$P_r=\frac{k'(k'+1)\ \ldots\ (k'+r-1)}{r!}p'^r(1+p')^{-k'-r} \quad (4)$$

Haldane (1941) shows that the log-likelihood equation for (4) is

$$N[\log_e(k'+m)-\log_e k']$$

$$=\frac{n_1+n_2+\ \ldots\ +n_R}{k'+1}+\ \ldots\ +\frac{n_R}{k'+R-1} \ldots (5)$$

where n_r is the observed frequency of r, and R is the maximum value of r.

Equation 5 gives fully efficient estimates of k and p. The equation may be solved by elementary methods (Haldane 1941) but the procedure is tedious and not ordinarily necessary. The procedure is to guess a value for k', evaluate both sides, and, by successive approximation and interpolation, carry the value of k' to the required number of decimal places, usually not more than four. It is convenient to make an initial approximation of k' by use of equation 2, where P_0 is estimated as the ratio of observed zero observations to total observations. For further details, as well as a simple numerical example, the reader is referred to Haldane (1941).

A less tedious but not fully efficient procedure is to estimate k by successive approximation to satisfy equation 2. The method and its efficiency as compared to the maximum-likelihood method are discussed by Anscombe (1949, 1950).

The negative-binomial distributions in this paper were first fitted using the log-likelihood equation 5 to estimate k. Some tabulation errors were later discovered in the data and all of the distributions were recalculated by estimating k from equation 2, with the exception of the distributions for haddock in depth zones II and III (table 5) and for ocean perch (table 9). The values of k were not materially changed by using the latter method which is, for these data, about 90-percent efficient. Since the first term of the expected series, using equation 2, is determined, there is one less degree of freedom than in using equation 5.

As pointed out in the text, the negative binomial approaches the Poisson as k increases. Some examples of the shape which the negative binomial may take as k increases with the mean m fixed are shown in figure 7. A value of k of about 0.1 would produce a curve similar in shape to the types found in this paper.

APPENDIX C

The logarithmic series

Fisher (1943) shows that the logarithmic series arises from the negative binomial distribution when, in equation 2, appendix A, we let $k=0$, write x for $p/(p+1)$, and replace the constant factor $(k-1)!$ in the denominator by a new constant factor, α, in the numerator. The expression for the expected number of species with r individuals is then

$$\alpha x^r/r \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where r cannot now be zero. The successive terms of equation 2 are, of course, the required series

$$\alpha x,\ \alpha x^2/2,\ \alpha x^3/3,\ \ldots\ \ldots\ldots\ldots (2)$$

The total number of species expected is

$$\sum_{r=1}^{\infty} \frac{\alpha}{r} x^r = -\alpha \log_e (1-x) \quad \ldots\ldots\ldots (3)$$

from which it is seen that the distribution is related to the algebraic expansion of the logarithm, hence its name.

The total number of individuals expected is

$$\sum_{r=1}^{\infty} \alpha x^r = \alpha x/(1-x) \ldots\ldots\ldots\ldots (4)$$

Letting S represent the total number of species observed and N the total number of individuals, we have from equations 3 and 4

$$S = -\alpha \log_e (1-x) \ldots\ldots\ldots\ldots (5)$$

$$N = \alpha x/(1-x) \quad \ldots\ldots\ldots\ldots\ldots (6)$$

so that both α and x may be determined if S and N are known. Fisher (1943) and Williams (1947) give tables of $\log_{10} N/\alpha$ in terms of $\log_{10} N/S$ for solving equations 5 and 6, given S and N. The computations are straightforward and the parameters x and α, as well as the terms of the expected series (equation 2), may be readily determined for a given set of data.

Fisher (1943) gives the following formula for the variance of

$$V_\alpha = \frac{\alpha^3 \left\{ (N+\alpha)^2 \log_e \dfrac{2N+\alpha}{N+\alpha} - \alpha N \right\}}{(SN + S\alpha - N\alpha)^2} \quad \ldots . (7)$$

The formula enables one to calculate the standard error of α but Anscombe (1950) points out that equation 7 is appropriate only under certain conditions of sampling, these conditions not being completely met in the census sampling. Anscombe gives the formula

$$V_\alpha \sim \frac{\alpha}{\log_e p} \quad \ldots\ldots\ldots\ldots\ldots (8)$$

which appears to apply to the conditions met in the census sampling, that is, comparisons of observations on different sorts of biological associations and comparisons of α from observations obtained in different years and with probable relative differences in abundance between areas and years. The variances of α use in this paper are estimated from equation 8.

APPENDIX D

A negative binomial distribution fitted to numbers of plaice eggs caught by a plankton net

The published data on sampling with plankton nets do not often give the total catches in successive tows, or sufficient data on number of tows with zero observations, to study the nature of the distributions encountered. Table 17 is a summary of the catches of plaice eggs in all stages of development in the southern part of the North Sea (Buchanan-Wollaston, 1923, table 3). The data were collected in 1914. Table 3 (Buchanan-Wollaston) indicates that 27 of the 50 stations yielded no plaice eggs in the plankton tows. The mean catch is 15.1 eggs with a standard deviation of 30.3.

Estimating k from formula 2, appendix B, we have

$$27/50 = (1 + 15.1/k)^{-k}$$

from which $k = 0.1292$.

The expected variance from equation 1, appendix B, is

$$15.1 = 15.1^2/0.1292$$

or 1779.9, as compared to the observed variance, 915.5.

The observed frequency of plaice eggs per tow and the frequency expected on the hypothesis of a negative binomial distribution are presented in table 18. The probability of obtaining a worse fit by chance for $\Sigma\chi^2$ with three degrees of freedom is somewhat greater than 0.60, so that the hypothesis of a negative binomial distribution of the data may not be rejected.

APPENDIX E

Proof, smaller sampling unit more efficient with heterogeneity present

When the variance is a function of the mean of a distribution, the effect of the size of sampling unit on the efficiency of sampling and on the precision of estimates cannot be expected to be obvious to the biologist. Experimental data confirming the validity of the efficiency of the smaller sampling unit, under conditions of heterogeneity, have been published by Fleming and Baker (1936), Beall (1939), and Finney (1946).

The precision of an estimate is defined as the reciprocal of its variance. Efficiency is defined in terms of the relative amounts of sampling required to give estimates of equal precision. If, for example, we sample area A with sampling unit a_1, and then sample area $A/2$ with sampling unit a_2 obtaining an estimate equally precise, we say that sampling unit a_1 is one-half as efficient as sampling unit a_2.

Heterogeneity is defined as a nonrandom condition where the presence of an item at any given point tends to increase the probability of another item being in its immediate neighborhood. Heterogeneity is to be distinguished from another type of nonrandomness in which items, through competition or whatever cause, act to repel each other so that they tend to fill the available space equidistant from one another. With heterogeneity, as here defined, the variance is always greater than the mean.

The problem of sampling with different sizes of sampling units has been examined by Beall (1939) whose statement of the problem is followed closely in equations 1 through 7 below. It is hoped that the proofs which follow in equations 8 through 10 will be helpful in clarifying some of the confusion which appears to exist concerning the problem.

Consider N strata of equal size and a sampling unit of area k. If the total area of the ith stratum is A, the total number of sampling units it contains is $A/k=M$. M will, of course, vary with the size of the sampling unit.

Let X be the total number of fish in the N strata. Let u_{ij} be the number of fish in the jth sampling unit $(j=1,2, \ldots M)$ in the ith stratum $(i=1,2, \ldots N)$. Let u be the average number of fish per sampling unit calculated over the entire N strata. Then

$$X=MNu \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Within the ith stratum, let the mean value of u_{ij} be u_i and the variance

$$\sigma_i^2=\frac{1}{M-1}\sum_{j=1}^{M}(u_{ij}-u_i)^2 \ldots\ldots\ldots (2)$$

Let m_i denote any number of samples taken in the ith stratum. Let the number of fish observed per sampling unit be $x_{i1}, x_{i2} \ldots x_{im_i}$ with mean x_i and estimated variance

$$S_i^2=\frac{1}{m_i-1}\sum_{j=1}^{mi}(x_{ij}-x_i)^2 \ldots\ldots\ldots (3)$$

M being equal for all strata, Beall (1939) states: "The best linear estimate of X, that is, the estimate with the minimum S. D. will be

$$F=M\sum_{i=1}^{N}x_i."$$

The standard deviation will be, when m_i sampling units have been drawn at random

$$\sigma_F=\sqrt{\left\{\sum_{i=1}^{N}\left(\frac{M_i(M_i-m_i)}{m_i}\sigma_i^2\right)\right\}} \ldots\ldots (4)$$

where M_i is the total number of sampling units contained in the ith stratum.

Since the strata are all equal in area, $M_i=M$ and $m_i=m$, so that equation 4 may be written

$$\sigma_F=\sqrt{\frac{M(M-m)}{m}\sum_{i=1}^{N}\sigma_i^2} \ldots\ldots\ldots\ldots (5)$$

MN is the total number of sampling units. Let $MN=M_o$. mN is the total number of samples taken. Let $mN=m_o$. Substituting in equation 5 we have

$$\sigma_F=\sqrt{\frac{(M_o-m_o)M_o}{m_o}\cdot\frac{1}{N}\sum_{i=1}^{N}\sigma_i^2} \ldots\ldots\ldots (6)$$

Since M_o and m_o are fixed, the accuracy of the estimate of F is determined by the average variance within strata:

$$\sum_{i=1}^{N}\frac{\sigma_i^2}{N}=\sigma_o^2$$

The sampling unit which gives the smallest value to σ_o^2 gives the greatest accuracy to F, the estimate of X.

With the number of strata and the fraction of the area to be examined fixed, σ_F may be supposed to be affected by an increase in the size of the sampling unit.

Let $\sigma_F=\sigma_F'$ with sampling unit $k=1$. Let $\sigma_F=\sigma_F''$ with sampling unit $k>1$. When $k=1$, $M=M'$, and $m=m'$. When $k>1$, $M=m''$, and $m=M''$. For each value of k, there will be a value of σ_o^2 and $M''/M=m''/m=1/k$. By elementary algebra, we obtain from equation 5

$$\frac{\sigma_F'}{\sigma_F''}=\sqrt{\sigma_o'^2}\div\sqrt{\sigma_o''^2/k} \ldots\ldots\ldots\ldots (7)$$

Proof that, with a Poisson distribution, all sizes of sampling units are equally efficient.—Consider the ith stratum. Let it contain M sampling units. Let the number of sampling units to be taken be m. Let F be the estimate of the total fish in the ith stratum. By (5):

$$\sigma_F=\sqrt{\frac{M(M-m)}{m}}\cdot\sigma_i^2\ldots\ldots\ldots\ldots(8)$$

Consider sampling unit $k' > k=1$. Since the area of the ith stratum is fixed, the total number of sampling units of size k' is M/k'. For equal efficiency, it is required $\sigma_F^2=\sigma_F'^2$ without increasing the total area of the sample taken, so the number of samples to be taken for $k' > k$ is m/k'. By equation 5:

$$\sigma_F{}^1=\sqrt{\frac{M/k'(M/k'-m/k')}{m/k'}}\;\sigma_i'^2\ldots\ldots(9)$$

where $\sigma_i'^2$ is the variance observed with the new sampling unit, k'.

The comparative efficiency of the new sampling unit will be equation (8) divided by equation (9):

$$\sigma_F^2/\sigma_F'^2=\sigma_i^2\div\sigma_i'^2/k'\ldots\ldots\ldots\ldots(10)$$

The means observed may be considered proportional to the size of the sampling units used, provided sufficient samples are taken, since both are sampling the same population density. So $x=x'/k'$, where x' is the mean observed with sampling unit $k'>k$. By definition of the distribution, $\bar{x}=\sigma_i^2$ and $x'=\sigma_i'^2=k'x$. Substituting in equation 10:

$$\sigma_F^2/\sigma_F'^2=\bar{x}\div k'\bar{x}/k'=1.0$$

Proof that the smaller sampling unit is more efficient if heterogeneity is present.—With heterogeneity as defined above, the variance is greater than the mean. As with the Poisson distribution, the means observed will be proportional to the size of the sampling units used, so that $\bar{x}=\bar{x}'/k'$. Because of heterogeneity, however, the variances are no longer proportional to the size of the sampling unit as in the Poisson distribution where $\sigma_i^2=\sigma_i'^2/k'$. For the negative binomial distribution and some other types of heterogeneous distributions, the relation between the mean and variance is of the type $\sigma^2=a\bar{x}+b\bar{x}^2$. We have, therefore, $\sigma_i^2<\sigma_i'^2/k'$ and it is immediately obvious from inspection of (10) that $\sigma_F^2/\sigma_F'^2$ will be less than 1.0.

It hardly needs to be pointed out that the application of this result to problems of heterogeneous sampling does not mean one's difficulties will be solved merely by taking the smallest possible sampling unit. Many practical factors will set a lower limit to the size of the sample it is desirable to take. In sampling with an otter trawl, for example, one would approach a point where more time would be consumed in lowering and raising the trawl than in fishing along the bottom. It must also be remembered that with the smaller sampling unit, minor sources of error may remain of the same magnitude and so become of proportionally greater importance with the smaller sampling unit.

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TABLES

TABLE 1.—*Distribution of values af χ^2 for paired tow catches of haddock, whiting, common skate, and total fish*

[Only hauls with $n_1+n_2>9$ are included]

χ^2	Proportion of cases expected	Haddock	Whiting	Common skate	Total fish
0–0.016	0.1	1	1	1	3
– .064	0.1	--------	1	2	1
– .148	0.1	2	1	4	3
– .275	0.1	1	1	1	1
– .455	0.1	2	--------	3	--------
– .708	0.1	--------	--------	1	4
–1.074	0.1	1	3	--------	3
–1.642	0.1	2	2	--------	4
–2.706	0.1	--------	5	1	2
–6.635	0.09	8	4	4	6
Over 6.635	0.01	33	42	13	82
Total cases	--------	50	60	30	109

TABLE 2.—*Values of total and mean χ^2 for haddock tows of different sizes*

[Only hauls with $n_1+n_2>9$ are included]

Number of fish	Number of paired tows	$\Sigma\chi^2$	Mean χ^2
10–49	19	184.4	9.70
50–99	8	120.3	15.04
100–149	3	181.7	60.57
150–109	4	187.4	46.95
200–299	2	25.7	12.85
300–399	2	90.1	45.05
400–499	3	452.7	150.90
500–599	--------	--------	--------
600–699	2	142.6	71.30
700–799	2	116.0	108.00
1136	1	168.9	168.90
1378	1	1.5	1.50
1714	1	49.1	49.10
2064	1	176.8	176.80
6731	1	885.2	885.20

TABLE 3.—*Distribution of catches per tow of haddock at two-tow stations*

Number per tow	Number of tows		Total
	Tow 1	Tow 2	
0	25	26	51
1	8	5	13
2	4	3	7
3	3	5	8
4	1	2	3
5	4	1	5
6	1	2	3
7	1	3	4
8	1	1	2
9	--------	1	1
10	--------	--------	--------
11	1	2	3
12	1	1	2
13	1	1	2
14	2	1	3
15	--------	1	1
16	--------	1	1
17	1	1	2
18	1	--------	1
19	--------	--------	--------
20	--------	--------	--------
21–25	2	2	4
26–30	3	1	4
31–35	2	2	4
36–40	3	2	5
41–45	--------	2	2
Over 45	23	22	45
Total	88	88	176

TABLE 4.—*Observed catch of haddock at two-tow stations and catch expected on the hypothesis of a negative binomial distribution*

Number of haddock/tow	Number of tows observed	Number of tows expected	χ^2
0	51	50.98	0.000
1	13	15.14	.302
2–3	15	10.39	2.045
4–7	15	11.21	1.281
8–14	13	11.15	.307
15–25	9	10.64	.253
43–4,586	47	66.49	5.714
Total	176	176.00	10.592

TABLE 5.—*Observed catch of haddock and catch expected on the hypothesis of a negative binomial distribution, depth zones, I, II, and III*

Depth zone	Number of haddock/tow	Number of tows observed	Number of tows expected	χ^2
I	0	35	34.99	0.000
	1–4	14	11.42	.583
	5–20	14	10.81	.942
	21–70	7	10.09	.946
	71–1,174	14	16.69	.434
Total	--------	84	84.00	2.905
II	0	37	41.50	0.488
	1–5	28	26.04	.148
	6–10	16	10.46	2.934
	11–18	11	10.54	.021
	19–30	15	10.64	1.787
	31–47	9	10.25	.152
	48–71	13	10.03	.879
	82–4,586	43	52.54	1.732
Total	--------	172	172.00	8.141
III	0	33	33.01	0.000
	1	11	11.41	.015
	2–3	15	13.40	.191
	4–6	16	12.39	1.054
	7–10	5	10.90	3.194
	11–16	9	10.91	.334
	17–25	13	10.41	.644
	26–42	13	10.41	.644
	43–91	9	10.01	.102
	91–161	3	4.15	.319
Total	--------	127	127.00	6.497

TABLE 6.—*Observed catch of common skate* (Raja erinacea) *and catch expected on the hypothesis of a negative binomial distribution, depth zones I, II, and III combined*

Number of skates/tow	Number of tows observed	Number of tows expected	χ^2
0	195	195.00	0.000
1–2	54	60.71	.742
3–4	26	27.93	.098
5–6	24	18.06	1.967
7–8	14	13.09	.136
9–10	12	10.06	.374
11–13	7	11.45	1.729
14–17	16	10.93	2.352
18–23	12	10.90	.111
24–33	8	10.43	.566
34–87	16	14.44	.169
Total	383	383.00	8.244

TABLE 7.—*Observed catch of whiting* (Merluccius bilinearis) *and catch expected on the hypothesis of a negative binomial distribution, depth zones II and III*

Number of whiting/tow	Number of tows observed	Number of tows expected	x^2
0	35	35.00	0.000
1	5	12.62	4.601
2–3	12	15.43	.762
4–5	6	10.71	2.071
6–8	10	12.20	.397
9–12	8	12.53	1.638
13–16	12	10.12	.349
17–21	9	10.55	.228
22–27	14	10.63	1.068
28–34	16	10.49	2.894
35–42	8	10.25	.299
43–52	16	10.95	2.329
53–2,690	148	138.52	.649
Total	299	299.00	17.285

TABLE 8.—*Observed catch of ocean perch* (Sebastes marinus) *and catch expected on the hypothesis of a negative binomial distribution, depth zone III*

[Includes 61 tows made in subareas adjacent to Georges Bank proper.]

Number of ocean perch per tow	Number of tows observed	Number of tows expected	x^2
0	59	60.24	0.026
1–2	15	13.84	.097
3–6	14	10.76	.976
7–14	8	10.29	.509
15–30	12	10.46	.227
31–60	14	10.24	1.380
61–890	26	32.17	1.183
Total	148	148.00	4.398

TABLE 9.—*Summary of tables 4–8, with degrees of freedom and probability associated with each* Σx^2

Species	Depth zone	Σx^2	d. f.[1]	Probability greater than
Haddock [2] [3]	I–III	10.592	5	0.05
Haddock	I	2.905	2	.20
Haddock	II	8.141	6	.20
Haddock	III	6.497	8	.50
Common skate	I–III	8.244	8	.30
Whiting	II–III	17.285	10	.05
Ocean perch [3]	III	4.398	5	.40

[1] See appendix B.
[2] Two-tow station data.
[3] Includes some tows made in subareas adjacent to Georges Bank proper.

TABLE 10.—*Number of tows, mean, variance, and standard deviation, for haddock catches by subarea and depth zone*

Subarea	Depth zone	Number of tows	Mean	Variance	Standard deviation
G	I	10	55.6	3,094	55.6
	II	8	19.3	255	16.0
	III	42	27.6	1,391	36.3
H	I	14	77.2	31,216	176.7
	II	14	53.3	11,015	105.0
	III	29	14.3	415	20.4
J	I	4	32.3	2,190	46.8
	II	24	230.3	123,956	352.1
	III	17	18.2	181	13.5
M	I	18	46.3	8,720	93.4
	II	42	288.0	633,397	795.9
	III	11	4.1	39	6.2
N	I	15	87.2	59,701	244.4
	II	39	68.5	13,717	117.1
	III	18	0.1	0	0.0
O	I	23	51.1	3,532	59.4
	II	45	16.5	1,153	34.0
	III	9	0.1	0	0.0

TABLE 11.—*Number of tows, mean, variance, and standard deviation, for whiting catches by subarea and depth zone*

Subarea	Depth zone	Number of tows	Mean	Variance	Standard deviation
G	I	10	57.9	14,038	118.4
	II	8	135.0	36,288	190.4
	III	42	75.6	5,050	71.1
H	I	14	235.5	108,481	328.4
	II	14	206.6	46,361	215.3
	III	29	153.9	35,267	187.8
J	I	4	164.8	18,644	136.6
	II	24	129.8	115,563	339.9
	III	17	154.6	38,841	197.1
M	I	18	60.8	3,012	54.9
	II	42	158.7	25,358	159.2
	III	11	376.3	256,151	506.2
N	I	15	113.7	13,951	118.1
	II	39	100.0	27,781	166.7
	III	18	187.8	395,583	629.0
O	I	23	134.9	42,828	207.0
	II	45	78.6	7,761	88.1
	III	9	13.4	294	17.1

TABLE 12.—*Frequency of occurrence of species with different numbers of individuals and expected frequency of occurrence on the hypothesis of a logarithmic series distribution, 1948–50*

a. DEPTH ZONE 1

Number of individuals	Species observed	Species expected	x^2	d. f.	Probability greater than—
1–4	12	10.180	0.325		
5–12	2	4.981	1.784		
13–34	4	4.947	.181		
35–96	4	4.989	.196		
97–250	6	4.605	.423		
251–10,433	15	14.298	.034		
Total	44	44.000	2.943	4	0.50

TABLE 12.—*Frequency of occurrence of species with different numbers of individuals and expected frequency of occurrence on the hypothesis of a logarithmic series distribution, 1948–50*—Continued

b. Depth Zone II

Number of individuals	Species observed	Species expected	χ^2	d. f.	Probability greater than—
1–4	10	10.453	0.020		
5–12	7	5.113	.696		
13–34	5	5.086	.001		
35–94	4	5.032	.212		
95–261	5	5.037	.000		
262–22,367	17	17.279	.004		
Total	48	48.000	0.933	4	0.90

c. Depth Zone III

Number of individuals	Species observed	Species expected	χ^2	d. f.	Probability greater than—
1–3	13	10.175	0.784		
4–8	6	4.905	.244		
9–21	7	5.139	.674		
22–53	4	5.033	.212		
54–133	7	5.001	.799		
134–17,893	12	18.747	2.428		
Total	49	49.000	5.141	4	0.30

TABLE 13.—*Frequency of occurrence of species with different numbers of individuals and expected frequency of occurrence on the hypothesis of a logarithmic series distribution, depth zones I–III*

a. Year 1948

Number of individuals	Species observed	Species expected	χ^2	d. f.	Probability greater than—
1–5	8	10.658	0.663		
6–16	6	5.118	0.152		
17–48	4	5.015	.205		
49–143	5	5.004	.000		
144–17,667	19	16.205	.482		
Total	42	42.000	1.502	3	0.60

b. Year 1949

Number of individuals	Species observed	Species expected	χ^2	d. f.	Probability greater than—
1–3	15	10.319	2.124		
4–8	4	4.977	0.192		
9–20	4	4.948	.182		
21–50	4	5.060	.222		
51–123	3	4.997	.798		
124–17,755	22	21.699	.004		
Total	52	52.000	3.522	4	0.40

TABLE 13.—*Frequency of occurrence of species with different numbers of individuals and expected frequency of occurrence on the hypothesis of a logarithmic series distribution, depth zones I–III*—Continued

c. Year 1950

Number of individuals	Species observed	Species expected	χ^2	d. f.	Probability greater than—
1–3	9	9.923	0.086		
4–8	4	4.786	.129		
9–21	4	5.013	.205		
22–54	5	5.021	.000		
55–18,496	28	25.257	.298		
Total	50	50.000	0.718	3	0.80

TABLE 14.—*Individuals (N), species (S), indices of diversity (α), and variance of α by depth zones and years*

Year	Depth zone	N	S	α	V_α
1948	I	5,837	27	3.661	0.4965
	II	16,496	34	4.096	.4934
	III	15,315	34	4.138	.5036
1949	I	11,246	33	4.178	.5290
	II	31,353	40	4.523	.5114
	III	15,138	37	4.564	.5630
1950	I	22,610	38	4.453	.5218
	II	17,610	35	4.195	.5029
	III	7,570	34	4.589	.6194
1948–50	I	39,693	44	4.888	
	II	65,459	48	5.018	
	III	38,024	49	5.551	

TABLE 15.—*Distribution of number of species caught per tow in each year (A) and the same with elimination of the first three tows following a change of net (B)*

Number of species per tow	Number of tows							
	1948		1949		1950		1951	
	A	B	A	B	A	B	A	B
0	1	1					3	
1	10	9						
2	12	7					3	1
3	11	10	5	5	2	1	1	1
4	11	9	5	1	6	5	9	6
5	10	5	9	5	5	5	8	6
6	18	17	13	11	10	8	7	5
7	17	15	13	10	11	10	5	5
8	12	11	11	7	15	14	10	10
9	5	4	18	17	14	13	15	15
10	13	11	9	5	12	9	8	8
11	11	10	14	10	17	13	12	11
12	3	3	7	5	10	8	5	5
13	4	3	11	8	9	9	6	6
14	2	1	4	3	1	1	3	3
15	2	1	2		1	1	1	
16			1	1	4	4	2	2
17					1	1	1	1
18					1	1		
Total	142	117	122	88	119	103	99	85
Mean	6.468	6.573	8.787	8.761	9.328	9.379	8.414	9.950

TABLE 16.—*Distribution of species and tows and the expected number of tows on a hypothesis of a Poisson distribution, 1948–51*

a. YEAR 1948

	NUMBER OF SPECIES									
	0–3	4	6	6	7	8	9	10	11 and more	Total
Observed tows	27	9	5	17	15	11	4	11	18	117
Expected tows	12.51	12.72	16.72	18.32	17.20	14.13	10.32	6.78	8.30	117
χ^2	16.780	1.088	8.215	0.095	0.281	0.693	3.870	2.627	11.340	44.989

b. YEAR 1949

	NUMBER OF SPECIES										
	0–4	5	6	7	8	9	10	11	12	13 and more	Total
Observed tows	6	6	11	10	7	17	5	10	5	12	88
Expected tows	5.60	5.94	8.66	10.84	11.98	11.56	10.13	8.06	5.89	9.33	88
χ^2	0.029	0.149	0.632	0.065	2.070	2.560	2.598	0.467	0.134	0.764	9.468

c. YEAR 1950

	NUMBER OF SPECIES										
	0–5	6	7	8	9	10	11	12	13	14 and more	Total
Observed tows	11	8	10	14	13	9	13	8	9	8	103
Expected tows	9.74	8.23	11.02	12.92	13.47	12.63	10.77	8.41	6.07	9.74	103
χ^2	0.163	0.006	0.094	0.090	0.018	1.043	0.462	0.026	1.414	0.311	3.627

d. YEAR 1951

	NUMBER OF SPECIES									
	0–5	6	7	8	9	10	11	12	13 and more	Total
Observed tows	14	5	5	10	15	8	11	5	12	85
Expected tows	9.60	7.63	9.83	11.12	11.18	10.01	8.32	6.27	11.04	85
χ^2	2.016	0.907	2.377	0.113	1.216	0.203	0.865	0.257	0.083	8.037

TABLE 17.—*Observed frequency of plaice eggs in 50 tows with a plankton net*

[Data from Buchanan-Wollaston, 1923]

Number of plaice eggs	Number of tows observed	Number of plaice eggs	Number of tows observed
0	27	36	1
1	3	38	1
2	1	54	1
4	3	56	1
5	1	72	1
8	2	95	1
14	1	121	1
18	1	123	1
22	1		
33	1	Total	50
34	1		

TABLE 18.—*Observed and expected frequencies of plaice eggs in 50 tows with a plankton net*

Number of plaice eggs	Number of tows observed	Number of tows expected	χ^2
0	27	27.00	0.000
1	3	3.46	0.061
2–5	5	5.23	0.101
6–16	3	4.94	0.762
17–50	6	4.94	0.227
Over 50	6	4.43	0.556
Total	50	50.00	1.707

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

EFFECT OF DISSOLVED ORGANIC SUBSTANCES ON OYSTERS

By Albert Collier, S. M. Ray, A. W. Magnitzky
and Joe O. Bell

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EFFECT OF DISSOLVED ORGANIC SUBSTANCES ON OYSTERS

By **Albert Collier** and **S. M. Ray**, *Fishery Research Biologists*, **A. W. Magnitzky**, *Oceanographer*, and **Joe O. Bell**, *Fishery Research Biologist*

In the course of prolonged and detailed studies of the effects of industrial wastes on oysters, *Crassostrea virginica* (Gmelin), continuous recordings of the activities of several oysters were made simultaneously. We noted that the oysters tended to behave in a parallel fashion which could not be correlated with any of the factors customarily measured. The work reported here presents our efforts to define the cause or causes. A preliminary paper on this subject (Collier, Ray, and Magnitzky, 1950), has demonstrated that an organic substance responding to the test for carbohydrates is associated with the activity of oysters.

There is a large body of information concerning the effect on oysters of those environmental factors which can be readily measured, including temperature, salinity, pH, turbidity, and oxygen content. Until recently, however, there have been no analytical estimates of continuous variations in the organic content of sea water and their relation to the activity of oysters. We were fortunate in having at our disposal a technique for estimating certain elements of the organic materials which react to the test for carbohydrates. J. Gordon Erdman suggested the method used here and adapted it to field conditions. The technique is described in the Appendix, page 182. It is important to note that all carbohydrate values are given in terms of arabinose equivalents, and do not necessarily reflect actual concentrations of carbohydrate substances.

It is our intent not to enter the argument concerning the utilization of dissolved organic materials by marine animals—an argument not yet closed (Korringa 1949)—but only to demonstrate the relation between the dissolved carbohydrates of sea water and the activity of oysters. This relation is discussed in the light of previous works on oyster physiology, together with some practical and theoretical implications.

TECHNIQUES

RECORDING THE ACTIVITY OF OYSTERS

We chose the simultaneous recordings of shell movements and pumping rates as the best available index of physiological activity, since both lend themselves to uninterrupted recording over long periods of time. The degree of shell gape alone could not be used, because gape is only the prerequisite to the filtration of water, and as long as it exceeds a critical point, the flow of water through the gills may vary considerably. The rate of removal of artificially introduced suspended materials gives a useful index of activity for short periods, for it can be measured quickly and apparently without affecting the oyster significantly. The method is not suitable for long-term studies, however, because it does not lend itself to the continued automatic recording of the oyster's activity in such a way that maximum detail of behavior is discernible in the record at any moment. Also, the carmine-cone and drop-counting techniques (Galtsoff 1928a and 1928b, Galtsoff et al. 1935), have limited value for this type of extended experiment not only because they can be used only for short-term observations, but also because they may seriously interfere with the neurosensory network controlling the water flow through the body of the oyster. In the carmine-cone method, the accumulation of carmine cannot be easily controlled, and its effect on the oyster cannot be measured as the experiment progresses.

While the pumping rate may not necessarily indicate feeding rate, this is not a legitimate objection to the use of the pumping rate as an index of physiological activity. Because the oyster takes its food from the water, there can be no doubt that the more water it passes through its filtering system, the more food it can get.

Note.—Albert Collier, S. M. Ray, and Joe O. Bell, United States Fish and Wildlife Service; A. W. Magnitzky, United States Navy Hydrographic Office.

Realizing that the pumping rate is a resultant of all the factors that influence the oyster, we accept it as the best available measure of physiological activity. The method used in measuring the pumping rate is described in the Appendix, page 183.

COLLECTING WATER SAMPLES

Sea water was pumped from the bay and supplied to the laboratory at Pensacola, Fla., as a continuous flow without storage, because it was desired to follow the changes in the bay water as they occurred.

During the course of the work, it became apparent that water samples were required at frequent intervals, owing to the wide and frequent variations in salinity and carbohydrate concentration noted in our preliminary tests. In September 1948 we began taking samples every 2 hours throughout the day and night, and in November 1949, the interval was shortened to 1 hour. The samples were collected by means of a special device described in the Appendix (fig. A–2).

CHARACTERISTICS OF CARBOHYDRATES

STABILITY

Since the effects of storage on these organic compounds, which we have defined as carbohydrates, were not known, it was necessary to determine their stability while in storage so as to establish the validity of values from samples which had been collected in the automatic sampler. We assumed that no significant change would occur during the intervals between analyses, and tested this assumption by collecting a series of triplicate samples from the laboratory sea-water supply (table 1). In each series, one was analyzed immediately, one was held overnight at room temperature, and one was held overnight in the refrigerator. The mean difference between the samples analyzed immediately and those held in the refrigerator was plus 0.007 milligram/liter, and for those held at room temperature was plus 0.094 milligram/liter. Since even the larger of these differences was within the range of error of our readings, we accepted this method of sampling as adequate, despite the delays inherent in making the determinations.

TABLE 1.—*Effect of standing time on carbohydrate concentration (mg./l.) of sea water at Pensacola, Fla., 1949*

Date	Hour	Immediate determination	Overnight in refrigerator	Difference	Overnight at room temperature	Difference
May 10	1200	15.4	15.5	+0.1	15.5	+0.1
	1400	15.5	15.4	−.1	15.4	−.1
11	1200	11.3	11.3	.0	11.2	−.1
	1400	12.6	12.8	+.2	12.8	+.2
16	1000	14.4	14.4	.0	14.4	.0
	1200	15.0	14.7	−.3	15.2	+.2
17	1000	16.3	16.3	.0	16.3	.0
	1200	16.3	16.3	.0	16.8	+.5
	1400	16.8	16.8	.0	17.0	+.2
18	1000	8.6	8.6	.0	8.7	+.1
	1200	5.8	6.0	+.2	6.0	+.2
	1400	6.6	6.6	.0	6.8	+.2
19	1000	6.3	6.1	−.2	6.3	.0
	1200	9.9	9.9	.0	9.9	.0
	1400	10.0	10.2	+.2	10.2	+.2
21	0800	10.7	----------	----------	10.7	.0
	1000	11.5	----------	----------	11.5	.0
	1200	11.2	----------	----------	11.2	.0
Mean	----------	----------	----------	+.007	----------	+.094

EFFECTS OF FILTERING AND CENTRIFUGING

Since the carbohydrate content of diatoms or other organisms present in varying numbers as particulate matter might cause erratic results in the carbohydrate analysis, we tested the magnitude of this factor, by making a series of tests on filtered and on centrifuged sea water, both separately and in combination. The results of these tests are shown below.

Carbohydrate concentrations of three samples before and after certrifuging [1] showed the following changes:

	Before	*After*	*Loss*
Sample 1	10.7	10.5	−0.2
Sample 2	13.9	13.7	−0.2
Sample 3	13.9	13.9	------

Carbohydrate concentration of four samples before and after filtering [2] showed the following changes:

	Before	*After*	*Loss*
Sample 1	11.5	11.3	−0.2
Sample 2	11.2	11.2	0.0
Sample 3	13.9	13.6	−0.3
Sample 4	14.1	13.9	−0.2

From these results it became apparent that each method was effective in removing particulate matter. A sample containing 10.8 mg. of carbohydrates to the liter was then centrifuged and found to contain 10.5 mg. to the liter. An aliquot of that same sample, when filtered, contained an identical amount, 10.5 mg./liter. The filtered sample, when centrifuged, showed no change. These experiments having demonstrated that either the 10-minute centrifuging or the filtering was sufficient to remove the particulate matter which might give erratic results, we adopted centrifuging as a standard part of the technique.

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[1] Centrifuged for 10 minutes at force 336. See Appendix, p. 182.

[2] Zeitz filter, porosity permitting 1.5 liters per hour at 40 millimeters vacuum.

VARIATIONS IN CARBOHYDRATE CONCENTRATIONS IN STANDING SEA WATER

We assumed that sea water with carbohydrates dissolved in it would also contain the organisms necessary for their production. Further, if the sea water were kept in jars in the laboratory, changes in species composition and in the numbers of organisms in it would be reflected in varying concentrations of the carbohydrates. If these compounds were of biotic origin, they would be expected to increase more rapidly with aeration than without; and if the producers were phytoplankton, production would be inhibited in the absence of light. In any case, the production of carbohydrates would not be expected if the causative organisms were removed by filtering. Accordingly, a set of experiments was designed to vary the conditions for growth and, by inference, establish which group of organisms was responsible for the production of the carbohydrates.

In experiment A we filled duplicate jars with fresh sea water. One was supplied with air by means of a small aquarium pump connected at the bottom to a sintered glass block; the other was left undisturbed. Samples were taken from the center of the jars by siphons, so calibrated that the water standing in them could be measured and discarded at each sampling. These jars were kept about 15 feet from the west windows of the laboratory and no lights were kept on at night, an arrangement which was followed with the indicated modifications in the other experiments of the series. In this experiment it was evident that the production of carbohydrates was stimulated by aeration (fig. 1–A).

Agitation, as produced by the aerating apparatus, might have stimulated multiplication of the micro-organisms, and so account for the differences indicated in experiment A. To test this we set up experiment B, in which the surface water was gently ventilated without agitation. Samples were taken near the bottom of the jar and from the surface of the water. The results show that the increased production of carbohydrates in the aerated water of experiment A was not due to agitation (fig. 1–B), but to the increased aeration. Here the carbohydrate concentration increased more rapidly and reached a higher concentration at the surface. It appears that part of the belated increase in the bottom concentration might have been the result of mixing due to convection currents in the jar.

In experiment C, filtered water was used to determine the sequence of changes when it could be assumed that the organisms which produce the substances had been removed from the water. As in experiment A, one jar was aerated and one was undisturbed. It was quite evident from the low carbohydrate concentration that the organisms producing these substances had been removed by filtration (fig. 1–C).

Experiment D was designed to demonstrate the role of light in the production of carbohydrates. The sequence of changes in both filtered and unfiltered sea water kept in the dark was followed. No significant changes in carbohydrate concentrations occurred in the absence of light (fig. 1–D).

From these experiments we may conclude that biotic activity is responsible for the production of carbohydrates, and that light and air create conditions favorable for the organisms producing these carbohydrates in sea water. It would be expected further that the responsible organisms are in part, if not altogether, photosynthetic, as indicated by the increased production in the presence of light. The effect of aeration is not so conclusive, for it is not known whether the air supplied carbon dioxide to plants, or oxygen to heterotrophic organisms (dinoflagellates).

RELATION OF CARBOHYDRATE CONCENTRATION TO SALINITY

We tabulated and averaged the carbohydrate-concentration values falling within salinity ranges of 2°/₀₀. Plotting of these averages shows an association between the concentration of carbohydrates and salinity (fig. 2). Between about 15°/₀₀ and 31°/₀₀ there is an apparent negative correlation between salinity and carbohydrates. From 7°/₀₀ to about 15°/₀₀ this relation is not clear and may not exist. The negative relation at the higher salinities may have been caused by the invasion of the carbohydrate-poor, high-salinity waters of the Gulf of Mexico into the carbohydrate-rich and low-salinity waters of Santa Rosa Sound. Whether this means that the correlation is due to the falling off in the carbohydrate values in proportion to the volume of gulf water intruding, or reflects an inverse relation between carbohydrate production and salinity in gulf waters, is not evident in these data. Lack of knowledge of the origin of these carbohydrates precludes speculation on the part that might be played by the salinity tolerance of the organisms responsible for their production. The association of carbohydrates with salinity illustrated could be the result of both physical dilution and biological interference due to salinity changes.

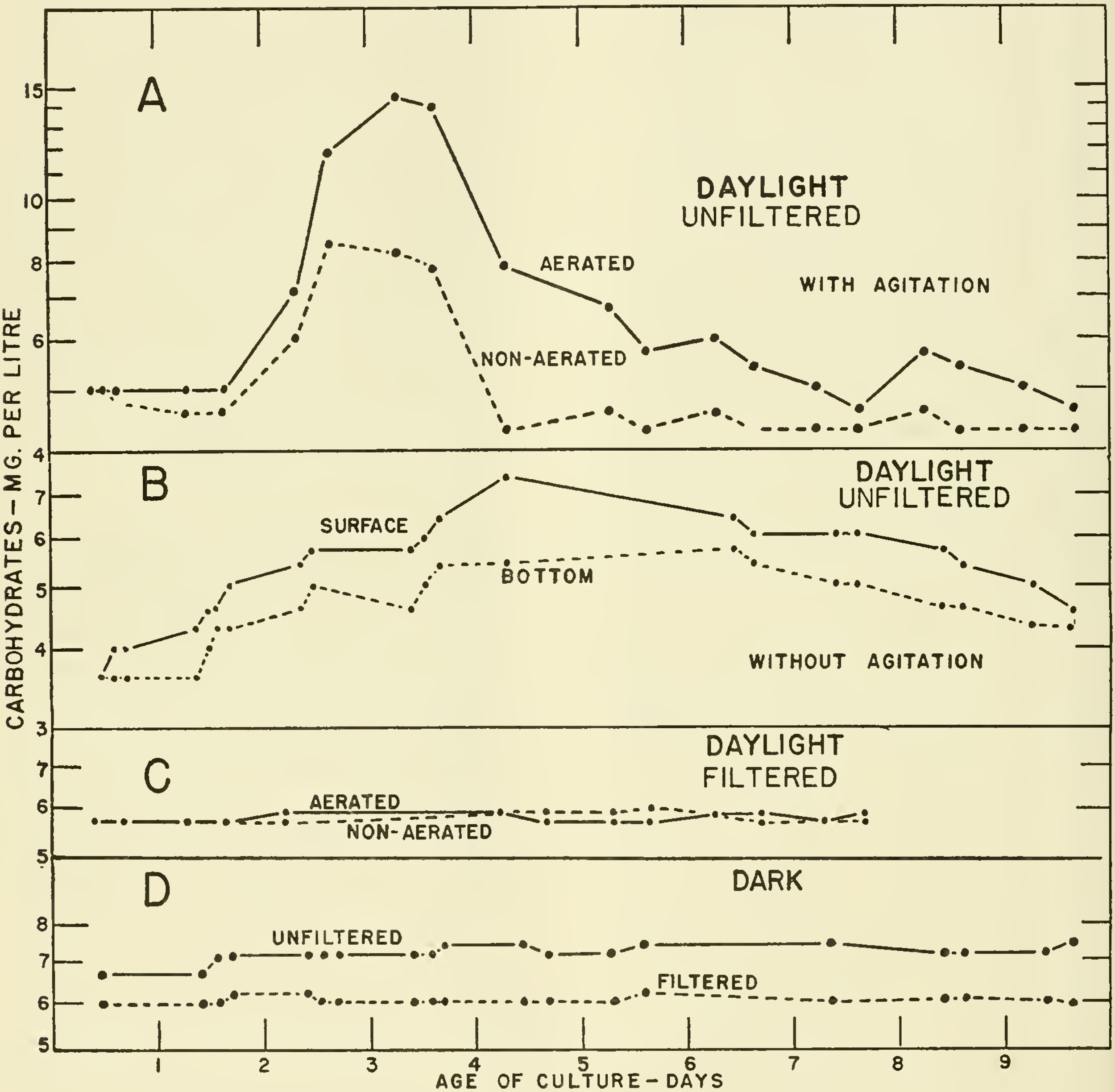


FIGURE 1.—Behavior of carbohydrates in standing sea water. A.—Exposed to daylight, unfiltered, with agitation. B.—Exposed to daylight, unfiltered, without agitation. C.—Exposed to daylight, filtered, aerated and nonaerated. D.—Kept in dark, filtered and unfiltered.

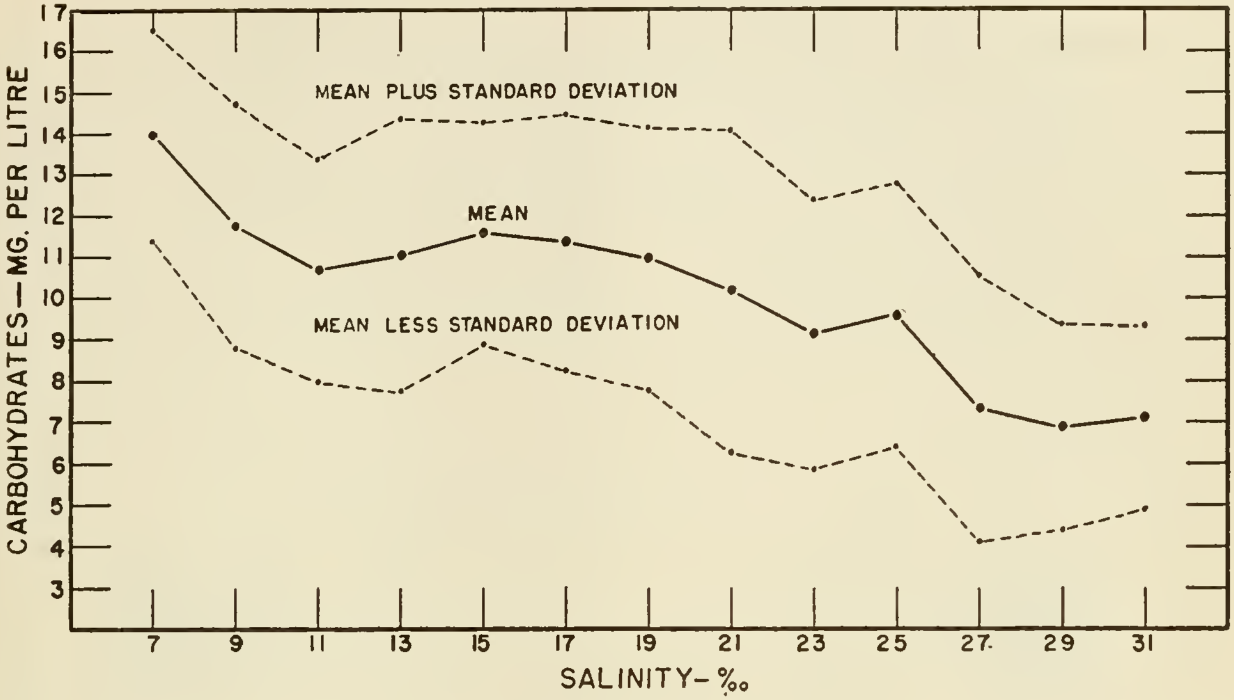


FIGURE 2.—Relation between carbohydrate concentration and salinity. The limits of the mean, plus and minus one standard deviation, are shown.

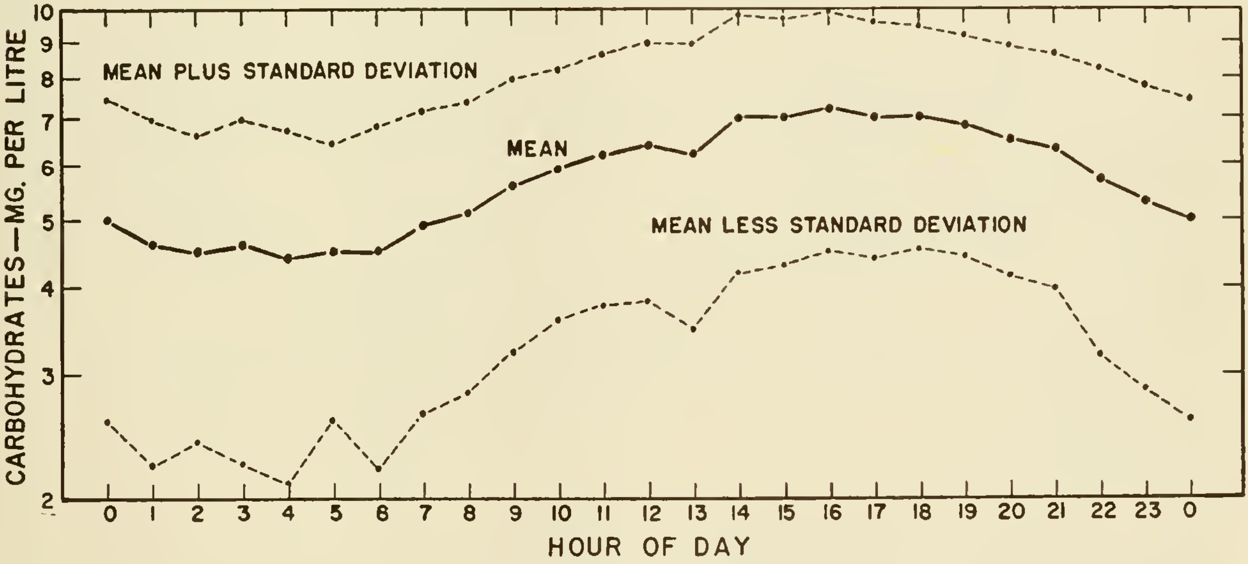


FIGURE 3.—Average diurnal variation in carbohydrate concentration for the period November 13, 1949, to May 30, 1950, plotted on semilogarithmic scale.

DIURNAL VARIATION

A distinct diurnal variation became evident when the logarithms of the carbohydrate concentrations were plotted against the hour of day for the period from November 13, 1949, (when the observations were increased from bihourly to hourly) until May 30, 1950. This cycle was evident whether the data were averaged monthly or for the entire period. The data of averages for the entire period are shown in figure 3; also plotted are the standard deviations computed at each hour.

From the curve (fig. 3) it is apparent that the concentration reaches a minimum at about 02^h00^m where it remains until about 14^h00^m; it then increases steadily to a maximum at 11^h00^m. This maximum is maintained until 18^h00^m, when the concentration begins a nocturnal decline.

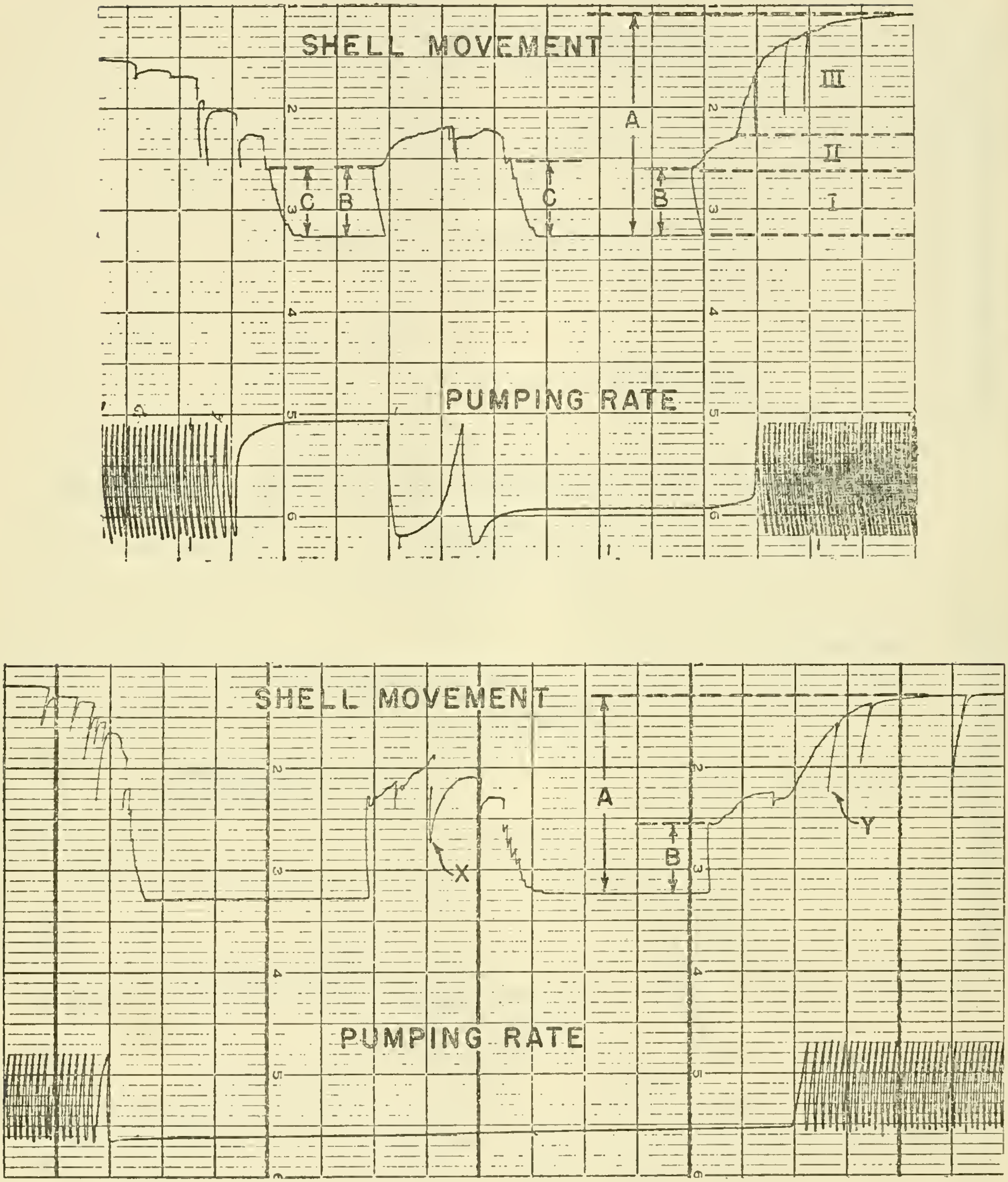


FIGURE 4.—Reproductions of actual records of shell gape and pumping rates, demonstrating the basic components of the shell movements of oysters. In each, *A* indicates the full amplitude of gape, *B* the opening movement of phase I, *C* the closing movement, which is always done in "steps." Lower figure shows two additional types of closures: *X* an abnormal one resulting from mechanical disturbance, *Y* a typical snap closure, probably to eliminate unwanted substances. Paper speed 2 inches an hour; vertical lines represent quarter-hour intervals.

THE OYSTER'S RESPONSE TO CARBOHYDRATES

ANALYSIS OF SHELL MOVEMENTS

In analyzing the activity of oysters, as shown earlier, it is necessary to consider separately shell movements and pumping rates. First, we have attempted to isolate and define the elements of the relaxation and contraction of the adductor muscle as reflected by recorded shell movements so as to relate oyster activity to carbohydrates.

Figure 4 illustrates representative shell movements. *A* represents the full gape of the oyster as recorded by the apparatus. This range of "openness," or gape, can be divided into three levels, or phases, which we designate as phases I, II, and III. Each phase has its physiological significance.

We interpret phase I as resulting from the activity of a single, special set of muscle fibers. It is characteristic of these fibers that they relax "all or none," and thus cause the almost instantaneous gape as typified by *B*. Notice that this set of fibers does not close the valves with a single sweep but in steps which have been designated as "treppe" (Galtsoff 1946). It is apparent that there is a distinct mechanism involved in this phase of shell movement. This phase is characterized, both opening and closing, by a more rapid response to external stimuli than are phases II and III.

We believe that phase II must be regarded as a delayed phase III, since it is a transition between phases I and III. This phase represents a testing period, and probably involves only the promyal and cloacal passages, since the oyster rarely will pass more than 6 or 7 liters of water an hour during this phase. It is probable that the musculature involved is the same as in phase III, but that there is a repressor mechanism which delays progress into phase III until certain environmental requirements are satisfied. Normally an oyster will not remain long in this phase. Figure 4 makes clear why we refer to any opening not going beyond phase II as a testing period.

In phase III, an oyster attains maximum gape and pumps the maximum amount of water. The pumping rate varies with conditions, so that it is essential to record both effluent and shell movement. Phase III, then, represents the full degree of valvular gape which under ideal conditions continues except for certain anomalies. This portion of the curve is broken at various intervals with partial closures indicated in figure 4 (lower) as *Y*. These anomalous closures might be termed "expulsion," or "snap," movements of the valves, probably to void accumulations of inert solids or irritating substances. These snap closures do not normally enter the zone of phase II, but when they do, the rate of reopening is much slower than when they do not. In figure 4 (lower), *X* indicates an abnormal closure resulting from a mechanical disturbance to the oyster. Note that the reopening is much slower than from the *Y* closure.

Each of the three phases has associated with it

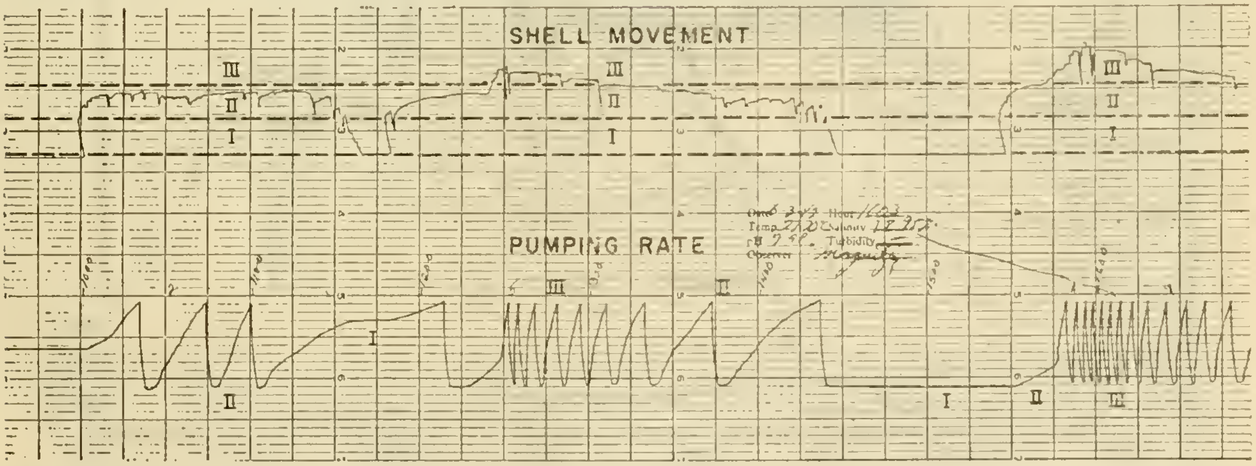


FIGURE 5.—The basic components of shell movements of oysters and their relation to pumping rates. Each cycle of the measuring box represents a minimum of 500 milliliters; the Roman numerals on the pumping rate curve correspond to the three phases demonstrated. Reproduction of actual record. Paper speed 2 inches an hour; vertical lines represent quarter-hour intervals.

definite characteristics of flow through the branchial system (here we arbitrarily include the promyal passage). Phase I may permit a slight flow or none at all; phase II involves some flow, although much less than does phase III. The relation between these phases and their respective pumping rates are typified in figure 5, which is a reproduction of an actual record showing rates of pumping in each of the three phases.

EFFECT OF CARBOHYDRATES ON PUMPING RATE

In these experiments the carbohydrate concentration in the laboratory sea-water supply varied widely. Variations over the entire range within a few hours were common; often variations were 100 percent within 2 hours. Such extreme variation precluded the use of averages in analyzing the data relating carbohydrate concentration to pumping rate.

The hourly effluents, therefore, were computed from pumping rates measured at the time the carbohydrate concentrations were measured. Samples for these carbohydrate determinations were taken from the inhalant side of the oyster, not from the sampling wheel (see Appendix, p. 183), which was located at some distance from the oyster. Over a long period of time using a number of oysters, we have found a positive correlation between the carbohydrate concentration and the pumping rate of the oyster, as shown in figure 6.

An interesting phenomenon, observed in the detailed study of the oyster's response to carbohydrates, is the testing period, illustrated in figure 7. Variation of the carbohydrate concentration at a temperature of approximately 25° C. is illustrated in the upper figure. Until 10^h00^m, the carbohydrate concentration was about 6 mg./l., followed by a rise within 2 hours to the 10 mg./l. level. At the beginning of the interval marked *A* the valves opened into phase II, during which period a small amount of water was passed through the oyster. At this temperature the carbohydrate level was too low to stimulate the oyster to further activity. After a short period of closure, another test was made at interval *B*. Within 30 minutes, the concentration of carbohydrates having risen while the valves were still in phase II, progress into phase III was induced as shown in intervals *C* and *D*. Similarly, but at

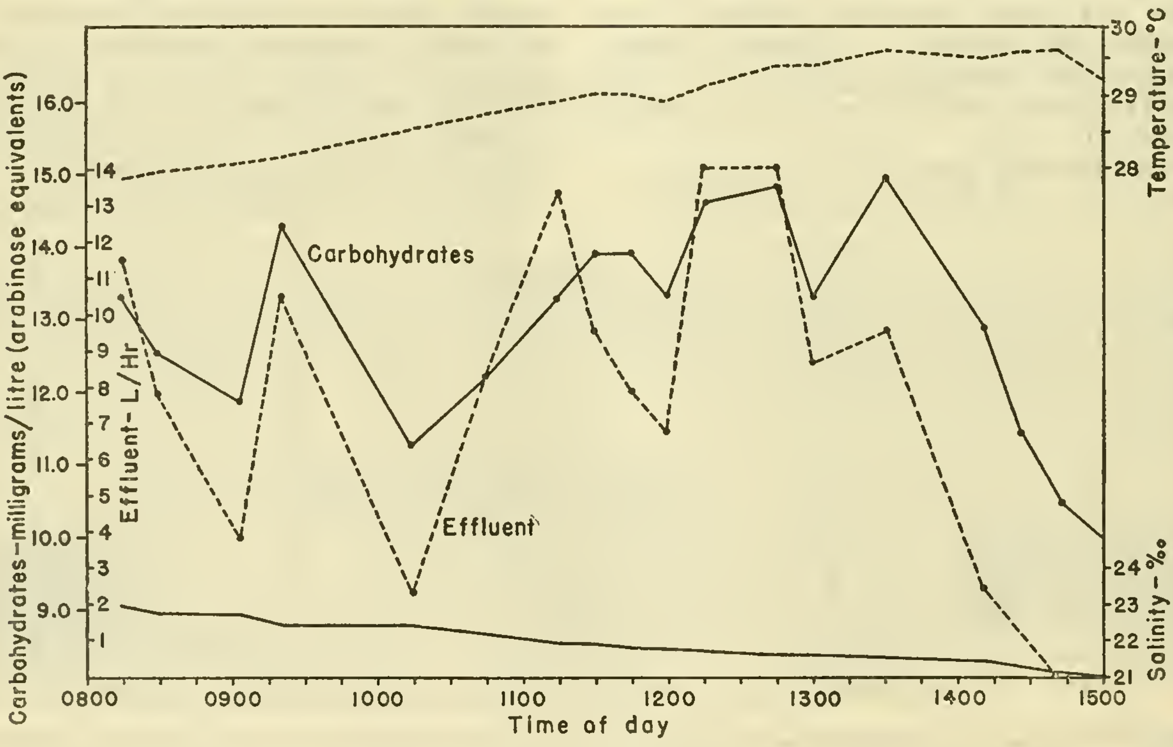
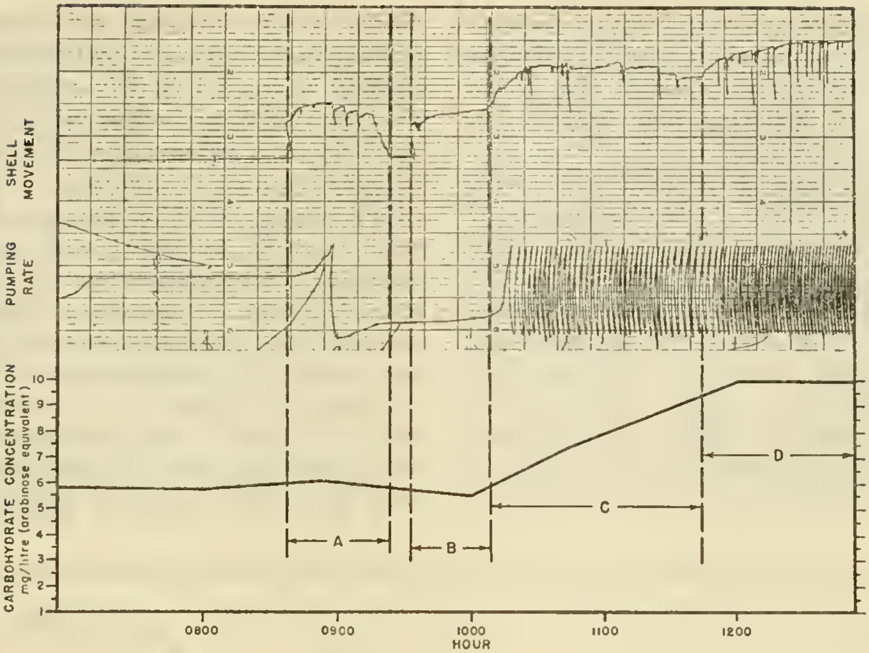


FIGURE 6.—Relation between pumping rates and carbohydrate concentrations. The pumping rates were determined at the moment the carbohydrate samples were taken. The mean carbohydrate concentration is 13.4, and the mean pumping rate 9.15 liters per hour. The correlation coefficient, 0.78, is significant at the 1-percent level.



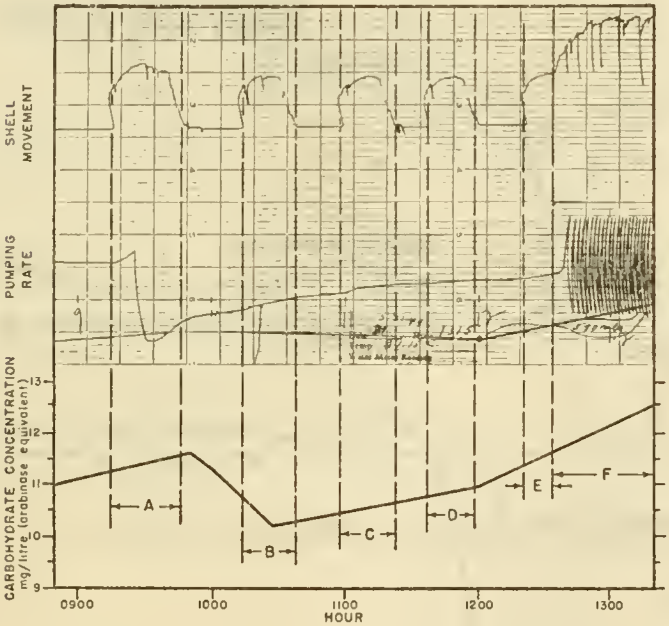


Figure 7.—Relation between activity of oysters and variations in carbohydrate concentrations at two temperature ranges. Upper figure at temperatures approximating 25° C., lower figure approximating 27° C.; salinity ranges 17° to 20°/oo The carbohydrate threshold for the oyster at 25° C. (upper figure) apparently approximates 6 mg./l. Testing periods are shown as intervals *A* and *B*, phase III as *C* and *D*. Lower figure (27° C.) shows four similar testing periods *A*, *B*, *C*, and *D*; on the fifth test, *E*, the carbohydrate concentration had increased sufficiently to induce phase-III pumping, interval *F*. This oyster, at the higher temperature, apparently had a much higher threshold level (approximating 12 mg./l.) than that of the oyster at 25° C. Reproductions of actual records. Paper speed 2 inches an hour; vertical lines at quarter-hour intervals.

an increased carbohydrate concentration because of increased temperature, the oyster recorded in the lower figure went from phase II into phase III at interval *E*, following four unfavorable testing periods *A* through *D*.

The association of increased pumping rate with a threshold level of carbohydrate concentration and the effect of increasing temperatures on this threshold level are obvious.

Having demonstrated the instantaneous pumping-rate response of the oyster to changing concentrations of carbohydrates, we examined the records of cumulative hourly pumping-rate responses to these changes. Figure 8 showing on a semilog scale the reaction of a typical oyster (No. 92), and of five oysters combined, to the changes in carbohydrate concentration, makes it evident that despite the stated limitations of this method to measuring the carbohydrate activity ratio, the relative changes in hourly effluents do parallel very closely the relative changes in carbohydrate concentrations. The low effluent rate preceding 18h00m on January 27 is coincident with phase-II pumping, and occurs with the carbohydrate concentrations below the threshold level for that temperature. With the rise in carbohydrate concentration above the threshold, the pumping rate increases to that of phase III.

Figure 9 illustrates, on a semilog scale, the relation of the average-cumulative-daily effluent to average-daily level of carbohydrate concentration, based on records of two to four oysters

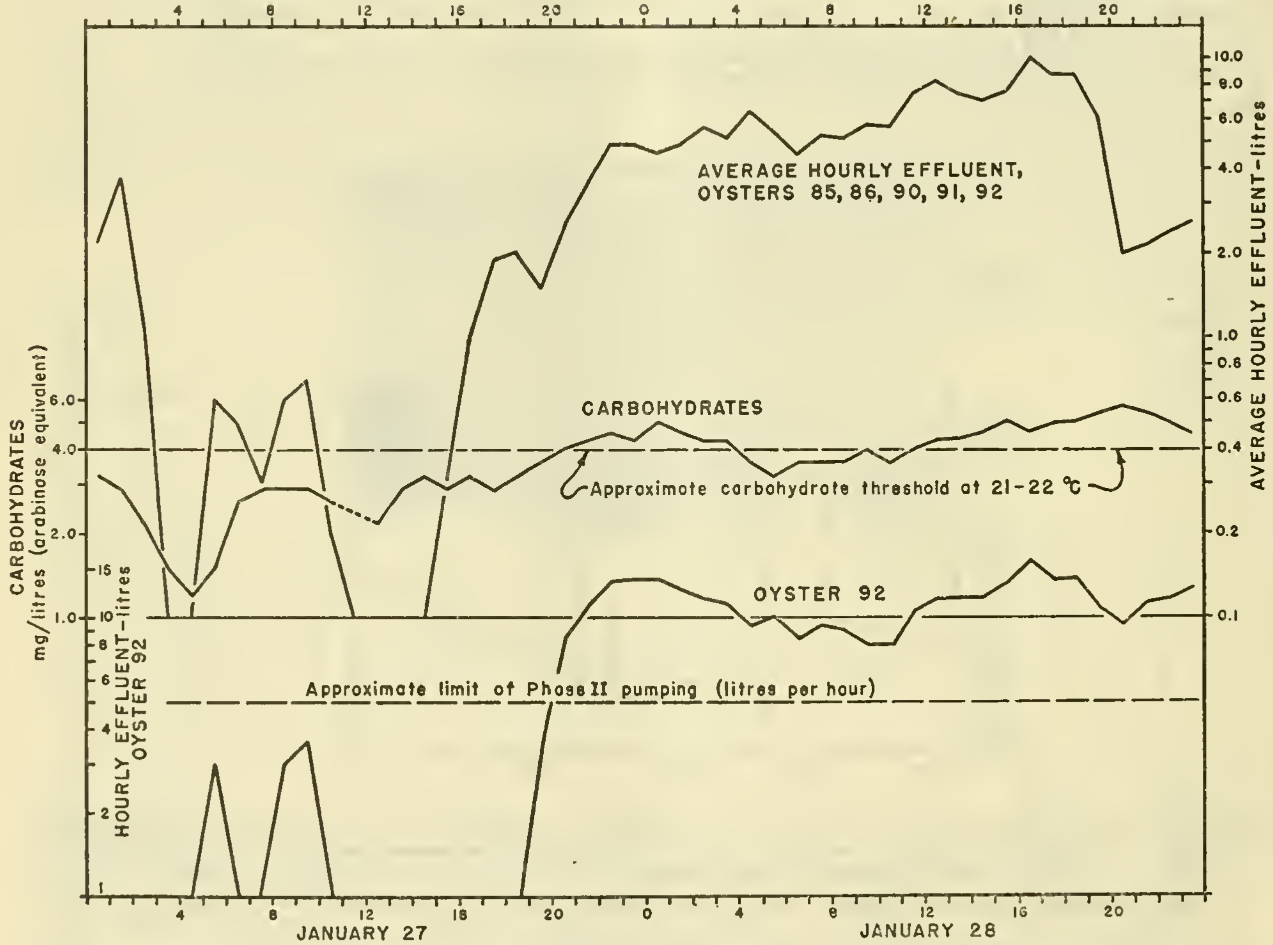


Figure 8.—The relation between carbohydrates and cumulative-hourly effluents over a 2-day period, plotted on semilog scale. The curve for an individual oyster is shown, together with the average values for all the oysters being recorded during the same period. In each case the hourly effluent went above the phase-II level when the carbohydrates went above 4 mg./l. During the twentieth hour of January 28, an external factor interfered. The oysters responded, but had begun to recover at the close of the period

available through a 30-day period. This comparison was made, despite its recognized limitation, to establish the relation over a long period. It is quite evident from an examination of this figure that such a definite relation does exist.

Figures 10 and 11 illustrate the relation that exists between carbohydrates and temperature as factors influencing the average pumping rate. Figure 10 is based on two defined temperature ranges, while figure 11 is based on a division according to season, i. e., the warm months, May 10 to November 13, and the cold months, November 13 to January 31, of the northern coast of the Gulf of Mexico.

It is apparent that water temperature above 25° C. are unfavorable for oysters in regions in which the production of the dissolved carbohydrates is low.

ASSIMILATION OF CARBOHYDRATES

The oysters can and do remove variable quantities of carbohydrates from the water. This has been ascertained by determining the amount of carbohydrate in the water before it enters the valves of the oyster and after it has passed through the body. The quantities removed do not seem to be related to any of the other measurable activities of the oyster, and, of course, the results could be affected by the oyster's waste metabolites, which are present in the exhalant water. The data of table 2 indicate that up to 50 mg./hour are removed. This is a significant quantity of such material, and assuming that all is utilized,

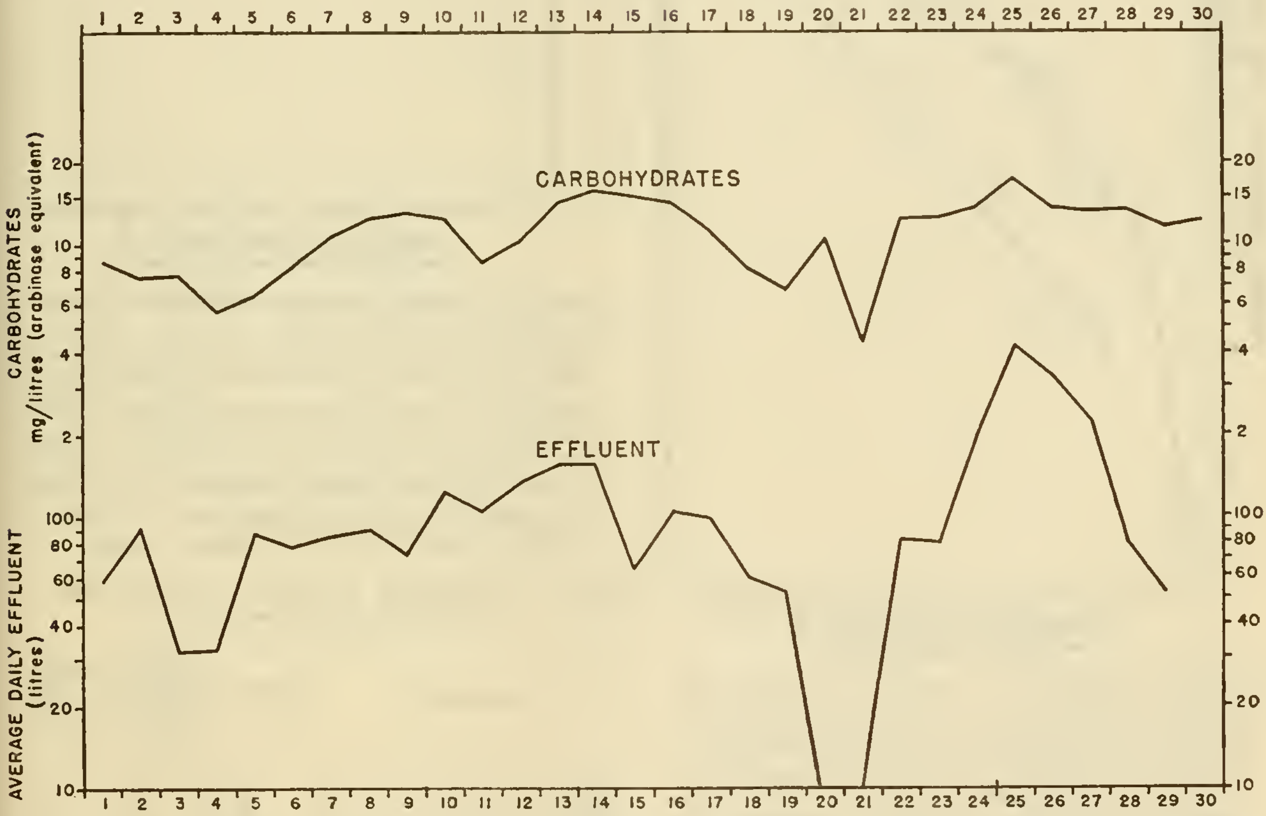


FIGURE 9.—Relation between carbohydrates and average-cumulative-daily effluents of two to four oysters over a 30-day period, June 1–30, 1949, plotted on a semilog scale. While data from four oysters were combined in establishing this curve, mechanical difficulties reduced the number to two during part of the time.

it represents an oxygen consumption[3] of approximately 50 mg./hour. Yonge (1928), in performing experiments on the mode of utilization of dissolved glucose, found that European oysters (*Ostrea edulis*) removed approximately 20 mg./hour. He felt that the removal took place in the stomach, and earlier (1926) had concluded that there was no evidence of any enzymes free in the gill mucus. This latter would not be necessary if the substance in question were adsorbed on the mucous train and carried into the alimentary tract.

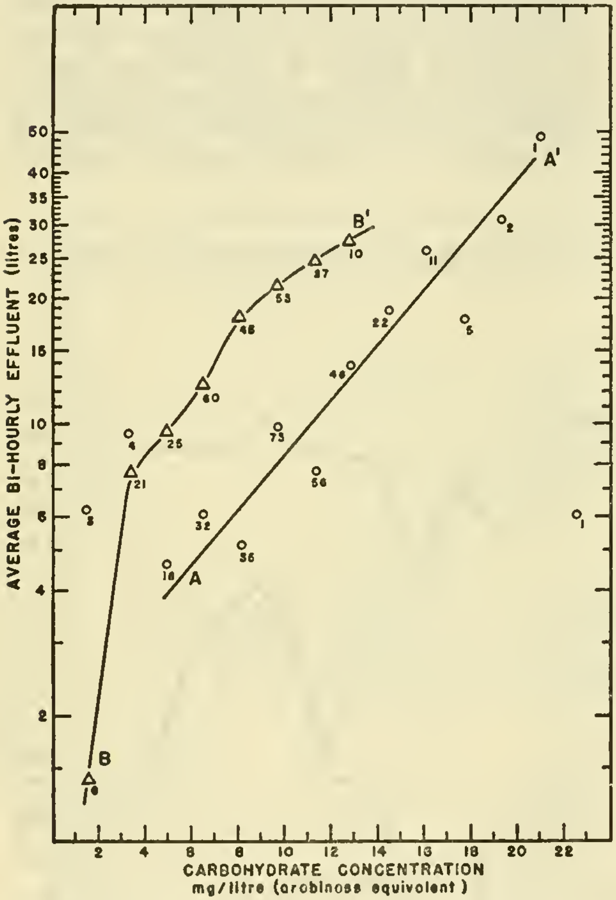


FIGURE 10.—The shift in the carbohydrate-pumpage relation due to temperature. The values are derived from the simultaneous observation of temperature, carbohydrate concentration, and bihourly effluent. Curve *A-A'* is for the temperature range 25° to 30° C., inclusive; curve *B-B'* is for 14° to 21° C., inclusive. The temperatures shifted from one range to the other so quickly that there were insufficient frequencies for analysis in the 22.0° to 24.9° C. bracket. The small figures at each point represent the number of samples from which the value is derived.

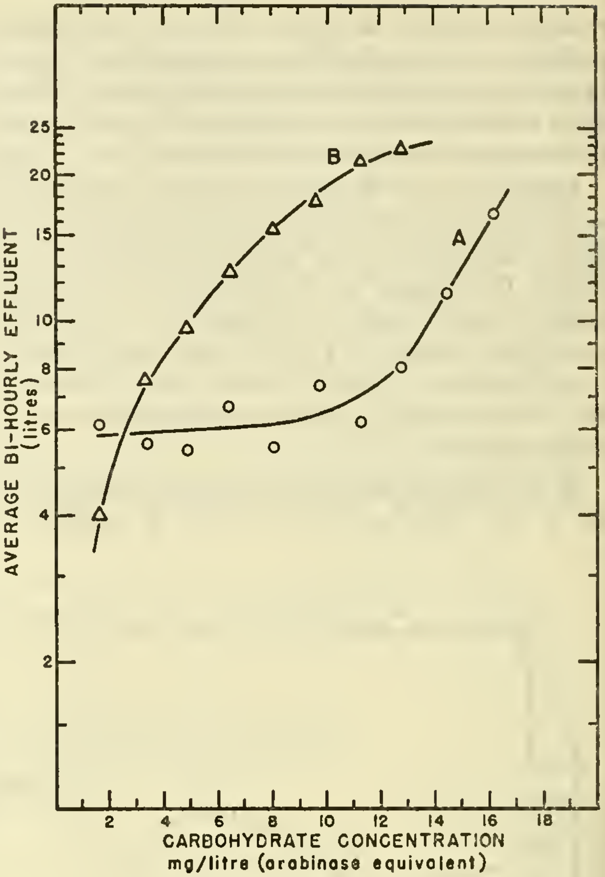


FIGURE 11.—Relation between carbohydrate concentration and the bihourly effluent of oysters. Curve *A* is derived from 3,891 bihourly observations on 12 oysters from May 10, 1949, to November 13, 1949. The flat portion of the curve represents the dominance of phase-II pumping (testing periods) at carbohydrate values of less than 12 mg./l. during the warm months. Curve *B* is derived from 5,464 hourly observations on 11 oysters for a period of winter temperatures, November 13, 1949, to January 31, 1950. Semilog coordinates.

TABLE 2.—*Removal of carbohydrates from sea water by oyster 74, May 24–June 11, 1949*

Pumping rate[1]	Temperature	Concentration of carbohydrates in sea water	Hourly rate of carbohydrate removal
L./hr.	*° C.*	*Mg./l.*	*Mg.*
12.7	26.1	12.1	11.4
13.9	25.9	12.1	15.3
17.1	26.7	7.3	13.7
17.6	25.9	10.5	10.6
24.4	28.4	6.6	21.7
24.6	25.9	11.2	24.6
25.2	27.2	8.7	22.7
25.2	27.2	6.3	15.7
26.4	28.8	11.0	50.2
27.9	28.5	9.1	22.3
29.3	28.0	8.2	35.2
33.4	27.5	10.5	16.7

[1] Some of these values were obtained while the oyster was going from phase I to phase II; therefore, the pumping rates shown do not necessarily reflect the correlation of pumping rate and carbohydrate concentration.

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[3] According to our later studies (Collier, Ray, and Magnitzky, manuscript in preparation), the oyster actually does utilize oxygen on a scale commensurate with this figure.

ANOMALOUS RESPONSES

The carbohydrate-temperature relation is not the only factor to which oysters respond. Others are involved, and they must often dominate the oyster's behavior pattern, and conceal the effects of the carbohydrates. As previously stated, it must be recognized that we do not know that the substances indicated as carbohydrates by the test are always true carbohydrates. Further, we cannot say which of the many carbohydrates are responding to the test, nor can we say which of the carbohydrates are represented. There is the possibility that the oyster is responding to a single carbohydrate which varies considerably, but whose variation may be completely hidden by other carbohydrates which may be far more abundant at times. Bell (1948) states that "numerous so-called glycogens in plants and animals may not be chemically identical with animal glycogens, which may quite well vary among themselves." Since glycogen is one of the carbohydrates, the significance is apparent.

Figure 12 demonstrates an extreme of variation between oysters in their responses to variations in carbohydrate concentrations. Note that oyster 88 was comparatively insensitive to carbohydrate changes during the first few days, especially on December 7. By comparison, oyster 87 was markedly responsive to the material throughout. Despite the anomalies (which may be due to the sampling difficulties previously pointed out), these figures illustrate the influence of consistently low carbohydrate levels, particularly during the winter period.

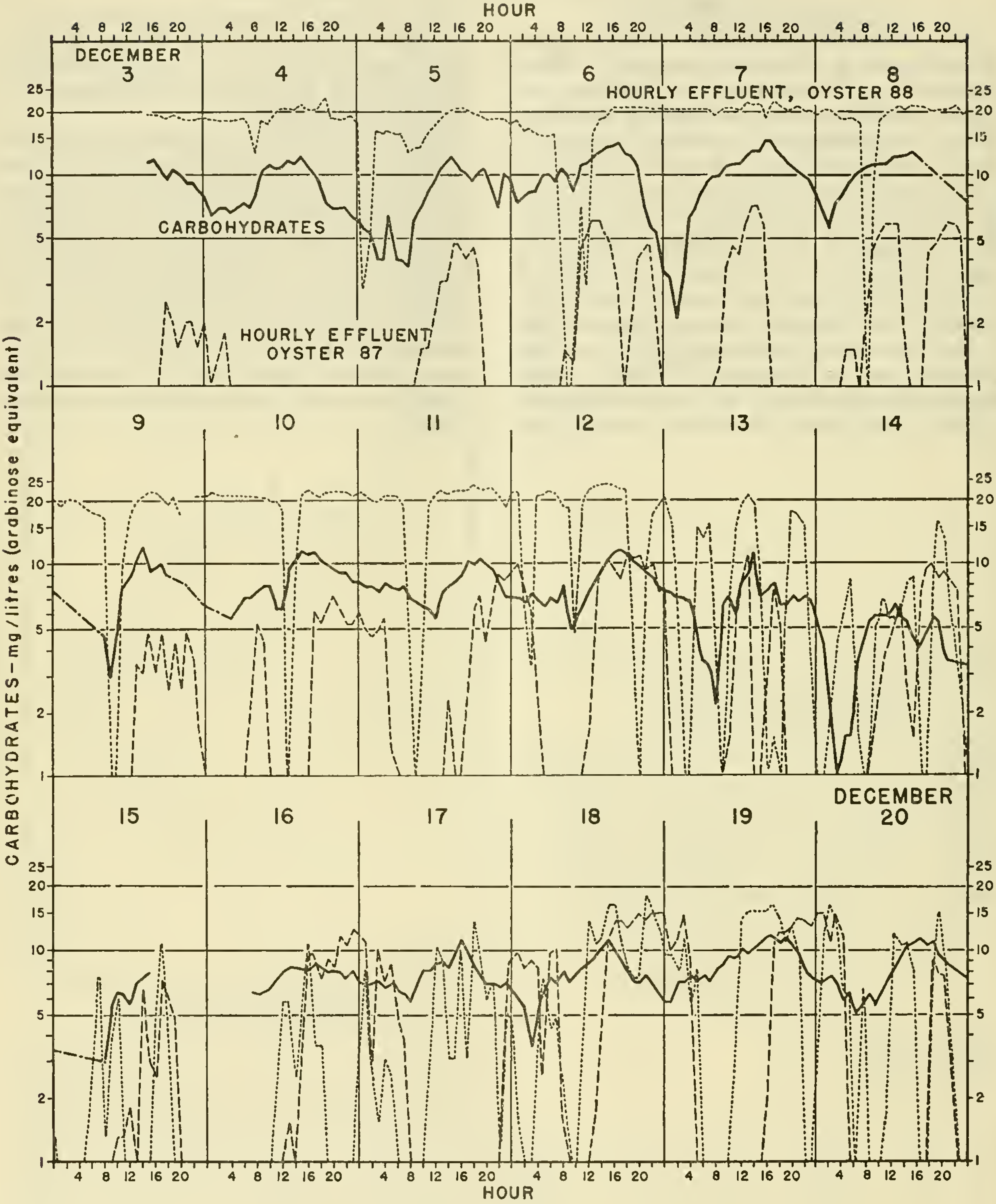

FIGURE 12.—Example of extremes in pumping-rate response of two oysters to a common carbohydrate concentration over an 18-day period plotted on a semilog scale. It is likely that oyster 88 had a glycogen reserve at the start, so was not as dependent on external nutrients as was 87.

SUMMARY

During prolonged and detailed studies of the effects of industrial wastes on oysters, *Crassostrea virginica* (Gmelin) at Pensacola, Fla., we noted that shell gapes and pumping rates of oysters under simultaneous observation behaved in a parallel manner as though responding to a common factor. It was found that this behavior pattern was related to the concentration of certain organic substances dissolved in sea water, and that these substances responded to the N-ethyl-carbazole test for carbohydrates.

The simultaneous recording of shell movements and pumping rates was chosen as the best available index of physiological activity for establishing this relation, since both lend themselves to uninterrupted recording over long periods of time. In analyzing these recordings, it became evident that shell movements and pumping rates are divided into three distinct levels, which we have defined as phases I, II, and III, each with its physiological significance. In phase I, there is an almost instantaneous gape on opening to about one-third of the maximum gape, a less rapid step closure, no pumping, and a rapid response to external stimuli. Phase II, the middle third of the total gape, must be regarded as a transition between phases I and III, represents a testing period, and probably involves only the promyal and cloacal passages, since the oyster rarely passes more than 7 liters of water an hour during this phase. In phase III, the oyster attains maximum gape and pumps the maximum amount of water. Because the pumping rate varies with conditions, it is essential to record both effluent and shell movement in interpreting the effects of varying concentrations of the dissolved carbohydrates. Certain anomalies within these phases were noted, including snap closures while in phase III. These closures usually do not enter phase II, but when they do, the rate of reopening is retarded.

An association between carbohydrate concentration and salinity was noted, but the significance of this relation remains obscure. It could be the result of physical dilution of carbohydrate-rich low-salinity inshore water with carbohydrate-poor high-salinity gulf water, or of the adverse effect of high-salinity water on the growth of the organisms creating the carbohydrates.

It was established that the oysters remove variable quantities (up to 50 mg./hour) of the carbohydrates from sea water.

Considerable variation in the response of individual oysters to the carbohydrates were noted. This would be expected, since the carbohydrate/temperature factor is not the only one to which oysters respond, and these other factors must often dominate the oyster's behavior pattern, concealing the effects of the carbohydrates. Then, too, the substances which respond to the N-ethyl-carbazole test may not all be true carbodrates, or the oyster may be responding to only certain of the carbohydrates within the carbohydrate complex, whereas the test responds to all.

The concentration of dissolved carbohydrates was found to vary widely in the sea-water supply. Because of this, the relation of carbohydrate concentration to pumping rate becomes obscure unless the pumping rate and carbohydrate concentration were measured simultaneously. A definite response of the oyster in the phase of opening and in the rate of pumping to the carbohydrate concentration was noted. Each oyster appears to have a threshold limit to the carbohydrates below which it will not pump. This threshold is raised with increasing temperatures. A correlation of 0.78, significant at the 1-percent level, was established over a long period of time using a number of oysters when the pumping rate and carbohydrate concentrations were measured simultaneously. Even when average-cumulative-daily effluents and average-daily-carbohydrate levels were compared, the relation between the two was striking. Because of the raising of the threshold level with increasing temperatures, it is apparent that water temperatures above 25° C. are unfavorable for oysters in regions in which the carbohydrate concentration is low.

During the course of these observations certain characteristics of these carbohydrates were investigated. It was established that no significant changes in concentration took place when held overnight either in the refrigerator or at room temperature; that the concentration first increased, and later decreased when exposed to daylight for prolonged periods; that this increase was affected by aeration; that, when filtered or centrifuged, or when held in the dark, no significant change in concentration took place. From these findings it became evident that the carbohydrates result from biotic activity.

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APPENDIX

ESTIMATING CARBOHYDRATES IN SEA WATER

The test for carbohydrates was developed by Dische (1927) with adaptations to suit our requirements by Erdman, who found that N-ethylcarbazole ($C_{12}H_8NC_2H_5$) was better suited for work with sea water than carbazole (Erdman and Little 1950). Further modifications were made for the particular type of electrophotometer (Fisher AC) used. All photometer readings were made with a green filter which bracketed the range of the peak absorptions of the dyes resulting from the use of the N-ethyl-carbazole reagent.

The reagent was prepared by dissolving 250 mg. of N-ethyl-carbazole in 250 ml. of prechilled 90-percent sulfuric acid (reagent grade [1]). It was made up in quantities to last not more than 48 hours and stored in the refrigerator. Use of distilled tapwater sometimes resulted in the development of a green color in the reagent, but distilled rainwater eliminated this difficulty. The tapwater was Mississippi River water from a small sedimentation and chlorinating plant. No explanation is offered for this reaction, but it is mentioned as a precaution to any who might apply the test. All glassware, including reagent bottles, should be thoroughly seasoned in sulfuric acid before being used.

Exposed to direct sunlight, the reagent will turn green and become valueless in approximately 5 minutes. It should be mixed in subdued light and stored in the dark.

In many cases where there is no carbohydrate present in the water the reaction will develop into deep green. In deep ocean waters this color has been found to be associated with high nitrate values; but if carbohydrates are present with the nitrates, the deep green will not develop.

The routine procedure was as follows: (1) The seawater sample was centrifuged for 10 minutes at a relative centrifugal force of 336. (2) A 2.5-ml. sample was drawn by pipette from the top of the centrifuged sample and put in a 25-ml. tube with 22.5 ml. of N-ethyl-carbazole reagent and hydrolyzed for 15 minutes at 70° C. ±0.5° C. A small chip of lint- and paper-free paraffin was dropped on the surface to exclude oxygen. (3) After hydrolysis, the sample was cooled for

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[1] Acid supplied in bottles with seals of cellulose derivatives was contaminated by them and was made unsuitable for this test.

15 to 25 minutes and transferred to a 23-ml. cuvette. The color density was measured and recorded as $-\text{Log } T$.

The densities thus determined were converted to equivalent arabinose in milligrams-per-liter by the use of a graph constructed from standard dilutions of l-arabinose. The general precautions pertaining to colorimetry were observed throughout. The data for a set of standards are presented in table A–1. The l-arabinose was checked for adsorption of atmospheric moisture by a series of weighings made over a period of 20 minutes at 5-minute intervals. No increase in weight was detectable on the analytical balance.

Table A–1.—(*−Log T*) *values for various concentrations of l-arabinose*

Test	1.03 mg. l-arabinose per liter	10.30 mg. l-arabinose per liter	20.60 mg. l-arabinose per liter	51.50 l-arabinosa per liter
No. 1	2.5	15.5	30.0	74.0
No. 2	2.5	15.5	31.0	74.5
No. 3	2.0	15.0	30.0	74.0
No. 4	2.5	16.0	30.5	74.0
No. 5	2.0	15.5	30.0	74.0
No. 6	2.0	15.5	30.0	73.5
No. 7	2.5	15.0	30.0	74.0
No. 8	2.5	15.5	29.5	74.0
No. 9	2.0	16.0	30.0	74.0
No. 10	2.0	15.5	30.0	74.0

MEASURING OYSTER ACTIVITY

The principle of the rubber apron originated by Moore (1908), and the constant-level chamber developed by Galtsoff (1926) were combined in this study to improve the accuracy of measurements of the pumping rate of oysters reported by Nelson (1936).

We found the attachment of the dental dam to the valves of the oyster was done most expediently with a small soldering nail and sticks of beeswax. The soldering nail was connected to a suitable rheostat and the voltage set to keep the soldering nail just at, or slightly over, the melting temperature of the beeswax. The beeswax was worked into small pencils and applied to the shell of the oyster with the point of the soldering nail. First, the wax was applied along the line of attachment of the rubber to fill the irregularities of the shell which could cause leaks. After this, a small wall of wax was built up and the rubber sealed to it. At the hinges and in the region of the palliobrachial fusion, small pads of pyrex wool (instead of cotton) were used as packing between the rubber membrane and the shell. The glass does not lose its resilience when wet, neither is it subject to organic decay on long exposure to experimental conditions. The oysters were held in position on Hopkin's stands (fig. A–1) and connected to the trough. To determine the amount of effluent, we used a simple box with an automatic siphon in the place of the usual dumping bucket (Collier and Ray 1948).

We acknowledge the great assistance of Drs. W. E. Hanson and J. G. Erdman of the Mellon Institute of Industrial Research, and we are grateful to W. K. Bowman, of the Gulf Research and Development Company, for providing us with excellent electric kymographs built to the specifications of our project. Some of the early records were made with a paper speed of 2 inches an hour, but this was later changed to 4 inches an hour. At the latter speed, we obtained 2 weeks of uninterrupted recording with superior amplification of detail.

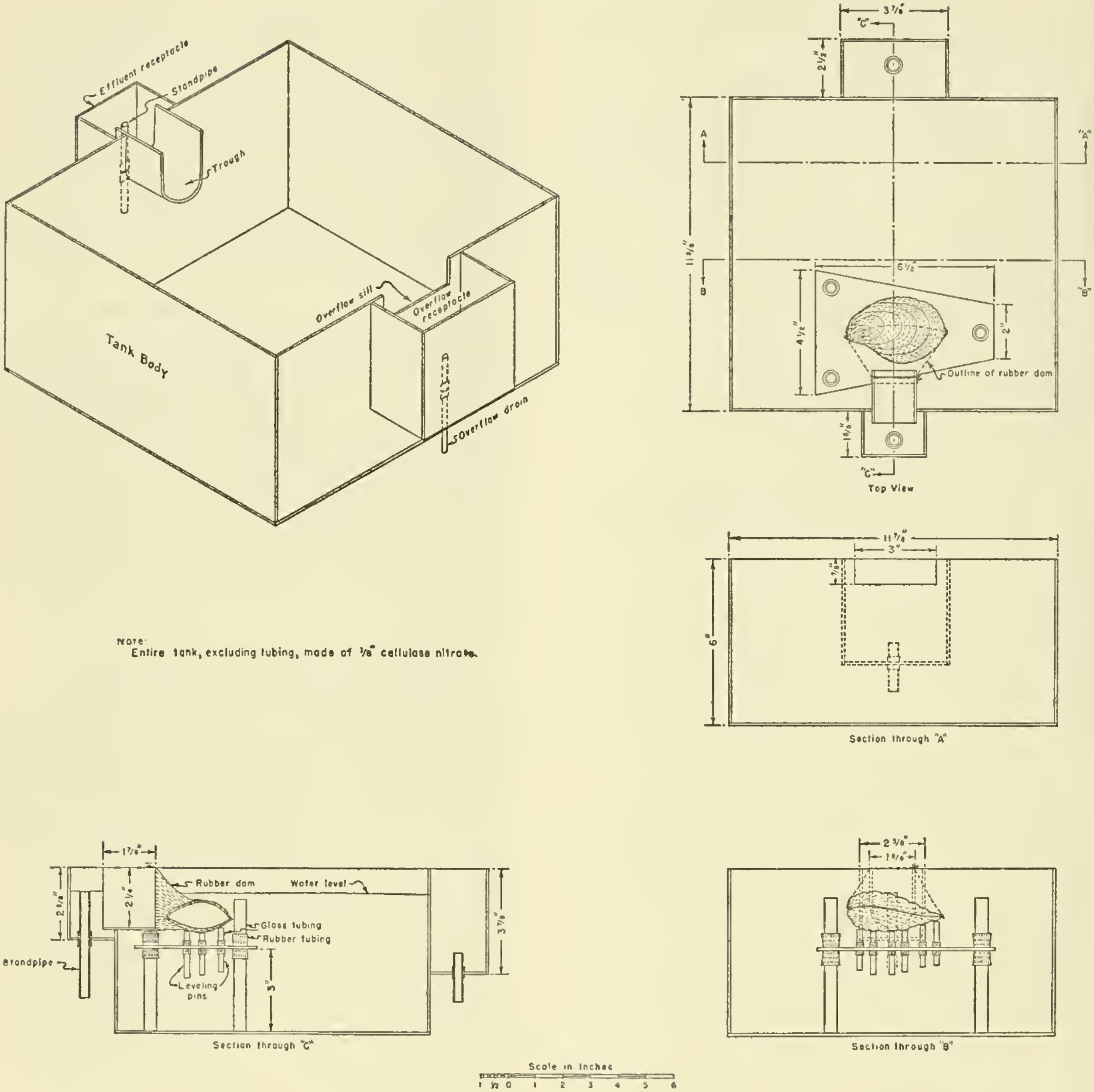
DESCRIPTION OF SAMPLING DEVICE

The sampling device (fig. A–2) consisted of a wheel (A) whose circumference revolved under a continuous stream of water (B), and thus caused the equally spaced tubes (C) to be filled. The interval of filling was regulated by the spacing of the tubes and the velocity of the wheel. The wheel was driven by a synchronous motor (D) whose velocity was 1 revolution in 24 hours.

The wheel was fastened to a vertical shaft by means of a flange; the shaft was suspended at (E) by means of a thrust bearing and set collar, and was connected to the drive shaft of the motor by a tubular coupling. In this manner, exposure of the motor and bearing suspension to salt water was minimized.

The waste water overflowed onto absorbent material, and this, in combination with the tight lid, kept the atmosphere within the chamber saturated. Evaporation was not sufficient to affect the accuracy required ($\pm 0.05^{\circ}/_{\circ\circ}$) for salinity determinations.

The apparatus as used by us gave a 15-minute composite sample every 1 or every 2 hours, as desired.



Note:
Entire tank, excluding tubing, made of 1/8" cellulose nitrate.

EXPERIMENTAL TANK USED IN MEASURING PUMPING RATE OF OYSTERS

FIGURE A–1.—Tank used in the experimental study of oysters. The oyster is fastened to the Hopkin's stand with beeswax at the ends of the small glass tubes. The water level at the top of the standpipe is finely adjusted so as to break over with the addition of two or three drops of water, yet not back the water into the tank body. The tube is cut with a carborundum saw and, once set up, it is never allowed to become dry, because the wetting property of the bacterial slime which accumulates there would be destroyed and the "sensitivity" of the tube lost.

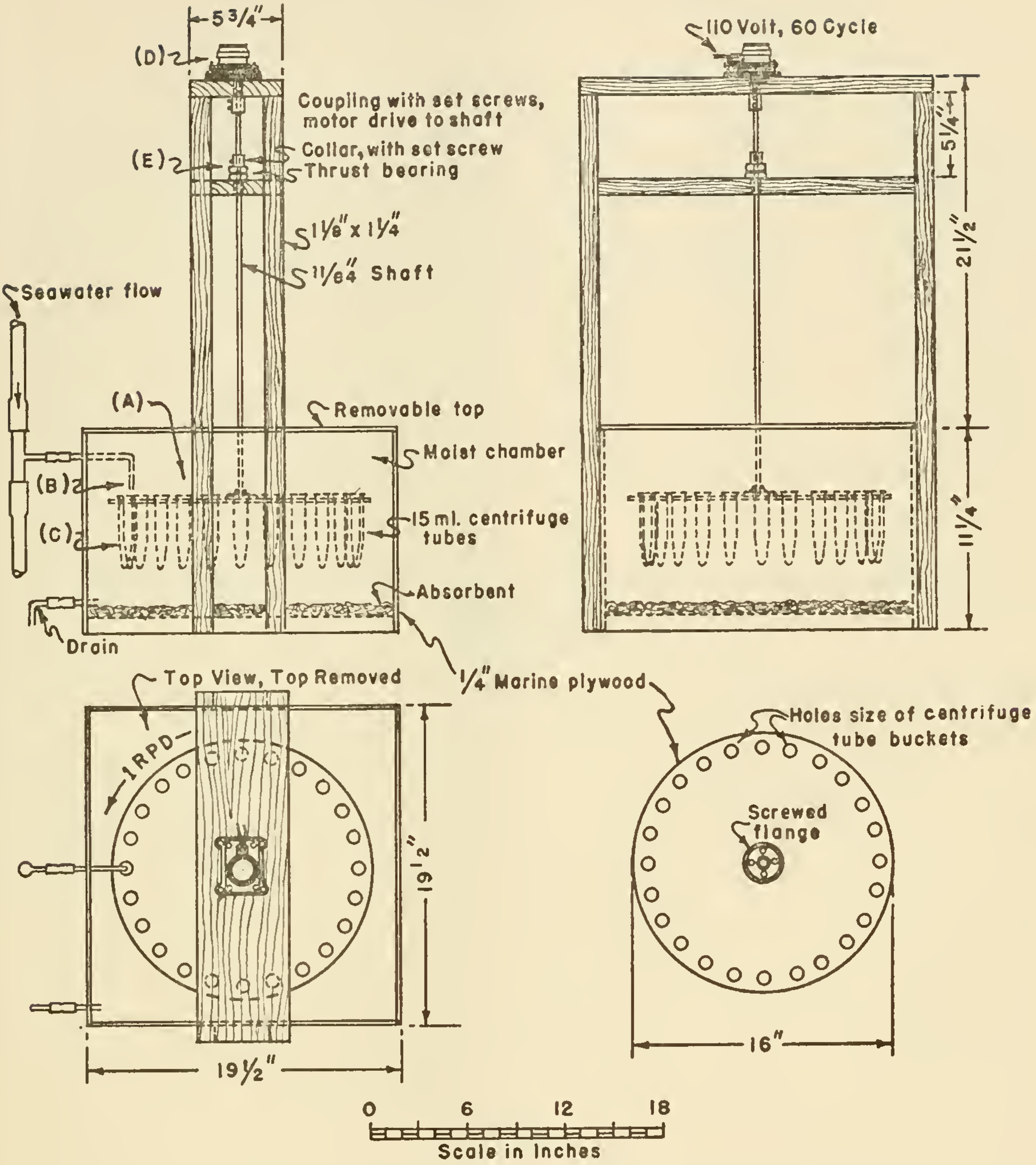


FIGURE A-2.—Device for automatically sampling water at hourly intervals. Operated by a synchronous motor, it was so designed as to rotate one of the 24 tubes under the inflow pipe each hour.

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DETERMINING AGE OF ATLANTIC SHAD FROM THEIR SCALES

By JAMES P. CATING

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DETERMINING AGE OF ATLANTIC SHAD FROM THEIR SCALES

By JAMES P. CATING, *Fishery Research Biologist*

Determining the age of fish is important in any study requiring knowledge of the age-class composition of the population. An accurate reading of shad scales was needed in the investigation of the shad fishery of the Atlantic coast, being carried on by the United States Fish and Wildlife Service to furnish information for fishery regulations to the Atlantic States Marine Fisheries Commission.

This paper presents criteria established for reading the age of shad (*Alosa sapidissima*) from their scales, in the hope that it may be of aid to other investigators. It is possible that the criteria given here, with minor changes, may be applied to other clupeids having scale markings similar to the shad's.

Fishery biologists have generally considered shad scales difficult to read, although most of them agree that some scales, especially from fish 4 years or younger, are easily read because the annuli are clear cut and proportionately spaced.

Leim's (1925) paper on the life history of the shad (*Alosa sapidissima*) in Canadian streams discusses the work by European investigators on age and growth of *Alosa alosa* and *Clupea finta*—very similar to *Alosa sapidissima*—in which they assumed the validity of the annuli as year marks. By plotting the length of scale against the length of the fish for a group of shad, Leim showed that the growth in length of the scale is almost proportional to the growth in length of the shad. He back-calculated the lengths of a series of shad at each winter of their life, and the calculated lengths agreed closely with length of fish as he had measured them at a given age. His total lengths plotted against age gave a curve that rose rapidly till the fourth year, and then gradually leveled off. In establishing the relation of length of scale to length of fish, he fulfilled one of the important requirements for establishing the validity of annuli as year marks on shad scales.

In his work on the fresh-water growth of shad, Hammer (1942) found that shad scales are constant in number and retain their identity throughout the life span of the fish. He did not attempt to age shad, but did show that back-calculated lengths determined for the fish at the time they left fresh water agreed with actual measured lengths of shad at that time.

Borodin (1925) presented a method of reading shad scales by counting the number of transverse grooves and dividing by 2 to get the age. Greeley (1937), however, has pointed out that this method gives erroneous results on Hudson River shad scales and his age determinations from easily read scales agreed closely with Leim's. Later workers, for instance Moss (1946), read only spawning marks on the shad scales and presented no data on the age of the fish studied.

These investigators did not establish criteria for separating the false from the true annuli on scales or for ascertaining the amount of absorption that takes place at the scale edge during the spawning migration of older fish.

I wish to acknowledge the assistance of members of the staff at the Beaufort Laboratory of the Fish and Wildlife Service who helped with this study through their constructive criticism and advice during the period of its development. These are C. E. Atkinson, G. B. Talbot, R. A. Fredin, and John H. Finucane who worked with me during the earlier part of the study and assisted in reading scales.

DESCRIPTION OF A SCALE

Figure 1 illustrates a scale from a Hudson River female shad that was 11 years old, 22½ inches long, and weighed 6½ pounds when taken. The anterior, sculptured portion of the scale comprises about three-fourths of the scale surface, while the posterior area (exposed portion of scale) consists of the remaining one-fourth of

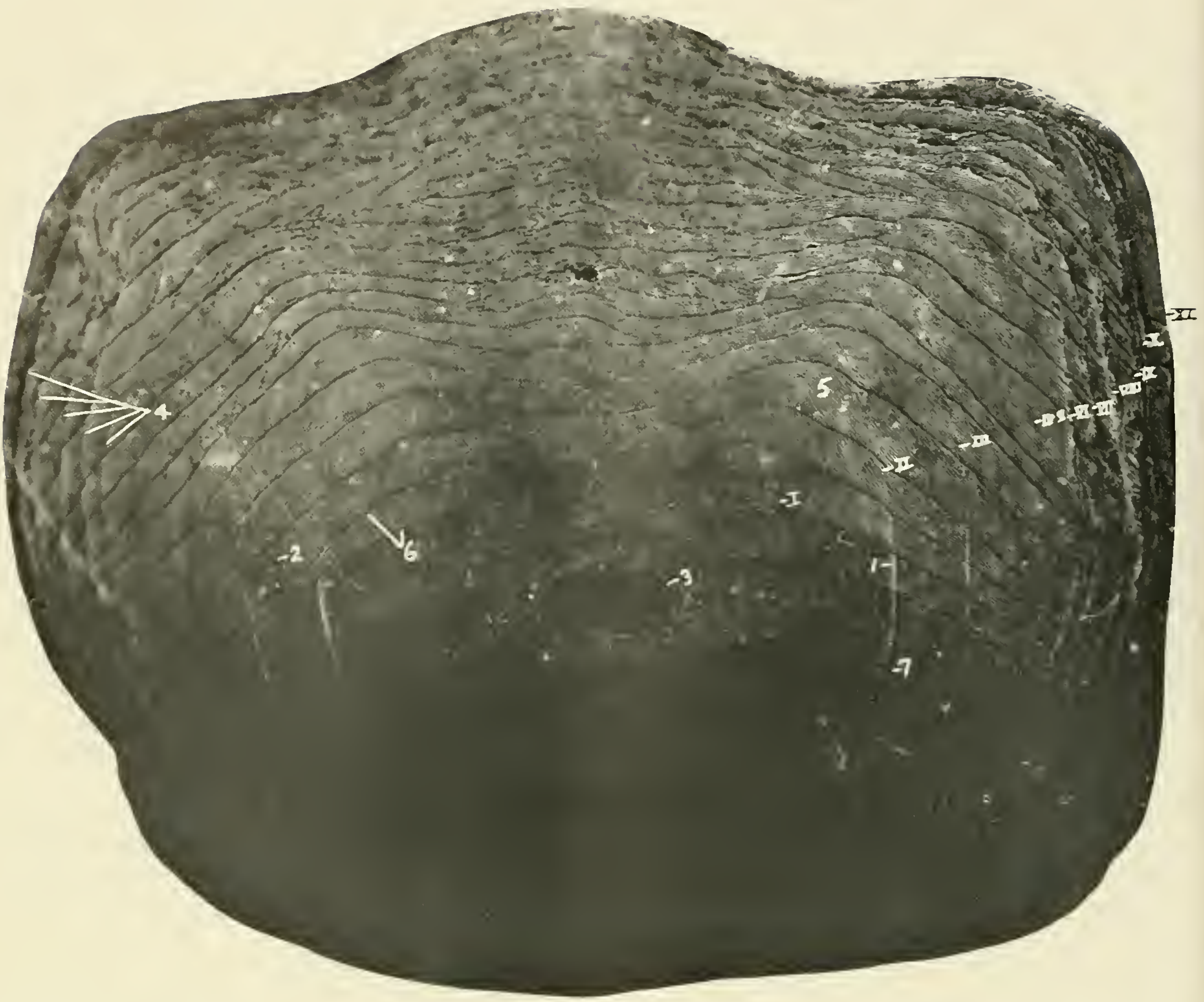

FIGURE 1.—A scale from a female shad measuring 22½ inches and weighing 6½ pounds. There are five annuli and five spawning marks, and the fish was spawning for the sixth time, which makes it 11 years old. The Roman numerals I through V represent the annuli, and VI through X the spawning marks. The Arabic numerals indicate the following: 1, annuli, or winter rings; 2, false annuli, or accessory rings; 3, fresh-water zone; 4, spawning marks; 5, striae; 6, transverse grooves; and 7, the baseline.

the surface area. The anterior portion has seven types of visible markings that are indicated by Arabic numerals on figure 1, as follows:

1. *Annuli, or winter rings.*—These are the lines seen on the surface of the scale following the contour of the periphery through both the anterior and posterior portions.[1] The annuli are usually most clearly seen in the lateral fields of the anterior portion near the baseline. On some scales they show very clearly on a diagonal line running from the center of the baseline to the shoulders of the scale.

2. *False annuli.*—These are also called accessory rings and are similar in appearance to true annuli. On easily read scales they do not show up as clearly as do the annuli, and are not usually found circling into the posterior portion of the scales studied. These marks make age determination from shad scales difficult. Notice the less-emphasized false annuli between the true ones on the scale shown in figure 2.

3. *Fresh-water zone.*—This is an important false annulus found on all shad scales and is laid down

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[1] For optical reasons, the posterior areas of the annuli cannot be seen in this photograph. They may, however, be seen during microscopic reading of the scale by changing direction of the lighting.

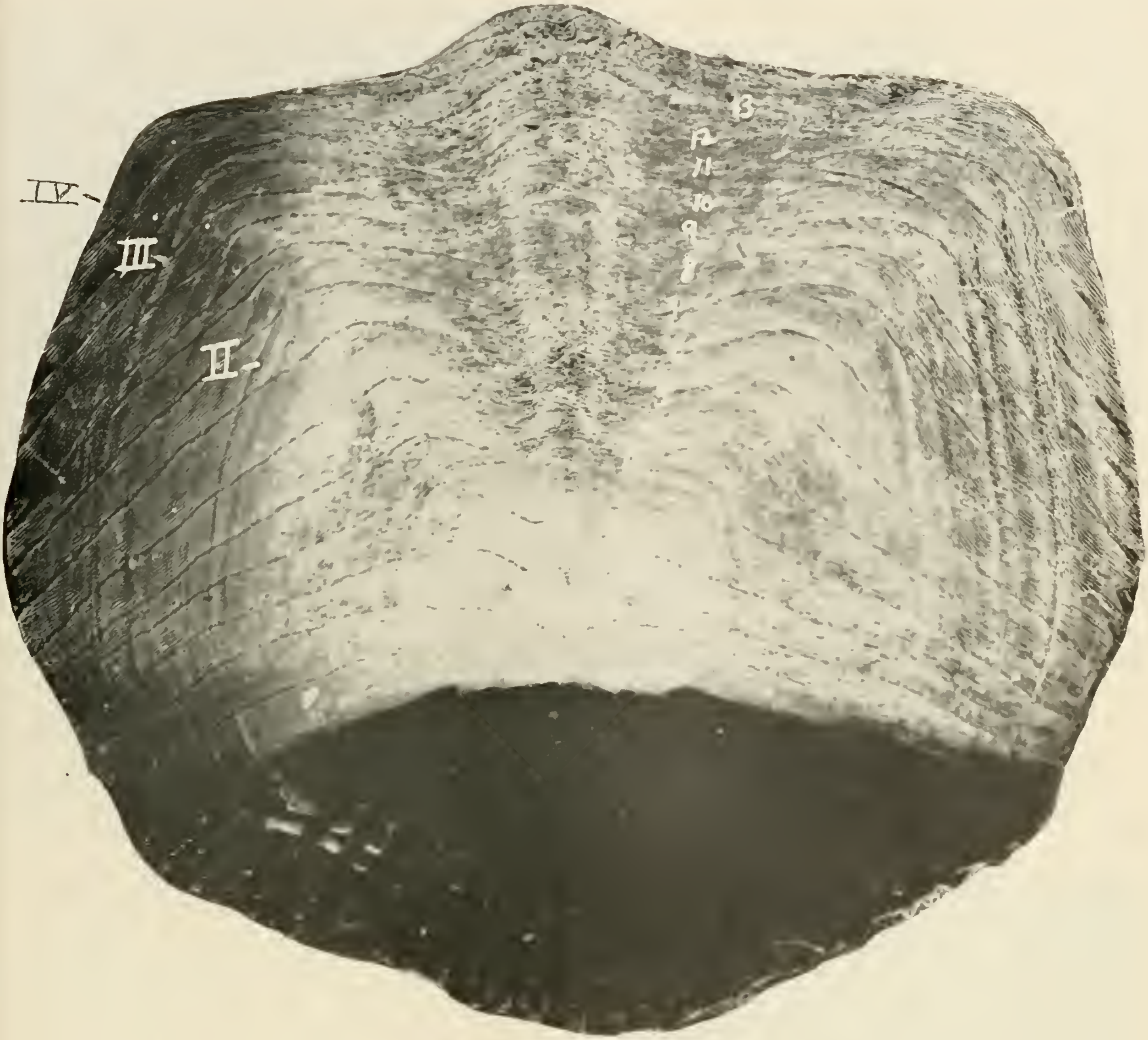

FIGURE 2. Scale from a 4-year-old male shad measuring 16.2 inches and weighing 2 pounds 8 ounces.

when young shad pass from fresh to salt water at the end of the first summer. Some workers apparently have called this the first winter annulus, but Hammer (1942) has shown that this line forms at the time of transition from fresh water in the parent river to salt water in the ocean when the shad are from 3 to 5 months old. Figure 3 illustrates the scale of a young Hudson River shad estimated to be 4 or 5 months of age and nearly ready to leave fresh water for salt water. If this shad had lived longer the scale, as seen now, would have formed the fresh-water zone of the larger scale.

4. *Spawning marks.*—These marks are scarlike rings extending around the anterior portion of the scale much as do the annuli, but unlike the annuli they extend only a short distance into the posterior portion of the scale. These marks are caused by absorption, or erosion, of the scale during the spawning migration into fresh water where little or no food is eaten by the adult shad. Figure 4 shows the condition of the edge of a scale from a shad just entering the Hudson River on the spawning migration. Notice the smooth margin. Figure 5 illustrates the irregular margin of a scale taken from a shad well up the river on the spawn-

ing ground. Figure 6 clearly illustrates a spawning mark (S. M.) formed a year previous to capture.

5. *Striae.*—These markings are fine ridges in the surface layer covering the anterior portion of the scale. They are very close together and run laterally across the scale in contour with the transverse grooves; figure 7 shows them clearly.

6. *Transverse grooves.*—These are distinct grooves in the surface of the anterior, sculptured portion, crossing it laterally on the same general contour as the striae, but spaced farther apart. Some of the grooves are continuous lines running from one edge of the scale to the other; others extend in from both sides without meeting in the center of the anterior field. Some of the grooves start as a single line at the edge of the scale and then branch to form two lines.

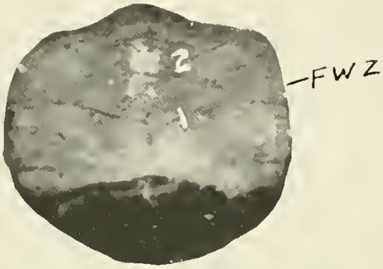

FIGURE 3.—Scale from a juvenile shad, probably 4 or 5 months old, caught while still in the river. There are only two transverse grooves. Had this shad lived longer the scale would have formed the fresh-water zone of the larger scale.

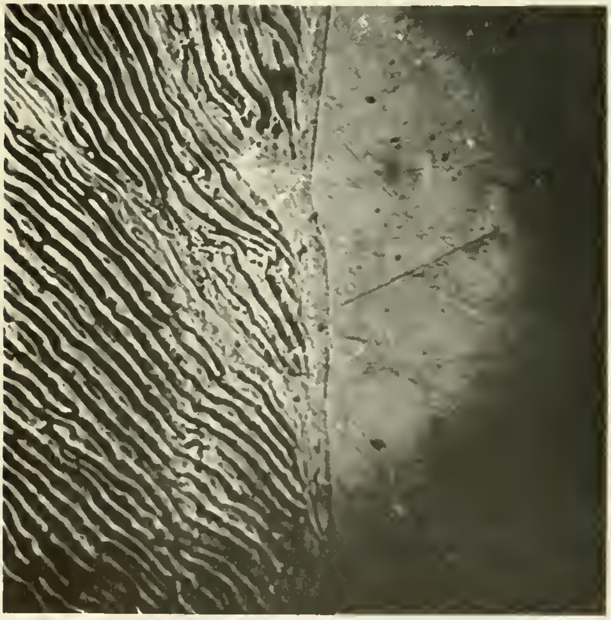

FIGURE 4.—Enlarged view of margin of the scale from a shad just entering the Hudson River on its spawning migration.[2]

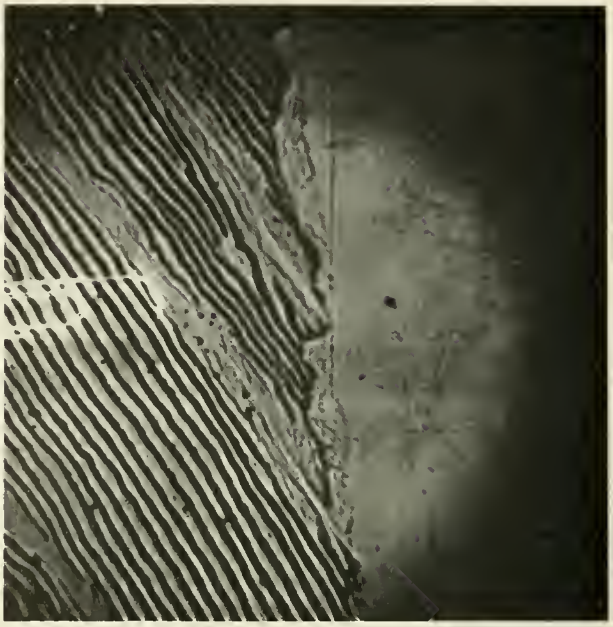

FIGURE 5.—Enlarged view of scale from a shad taken on the spawning ground after a period in fresh water.[2]

7. *Baseline.*—In this paper the baseline is considered to be the first transverse groove on or just anterior to the demarcation line between the anterior and posterior fields of the scale (also see A in fig. 8).

PREPARING AND READING SCALES

The scales used in this study were collected during the spring of 1950, from Hudson River shad, for use in age, growth, and mortality studies. Many of the scales taken could not be used, either because they were regenerate scales (fig. 9), or because they were asymmetrical and could not be read. Four hundred nonregenerate and symmetrical scales were chosen at random from the collection. Twenty scales, 2 each from 10 fish, were impressed on individual 3″ x 5″ plastic sheets using pressure and heat. Some scales were mounted in glycerine jelly and polyvinyl alcohol on glass slides to compare their readability with scale impressions on plastic. As far as we could determine, the one method is as good as the other, but since plastic impressions are easier to handle and less bulky to file, this method was used.

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[2] Photographs from an unpublished manuscript of Louella E. Cable.

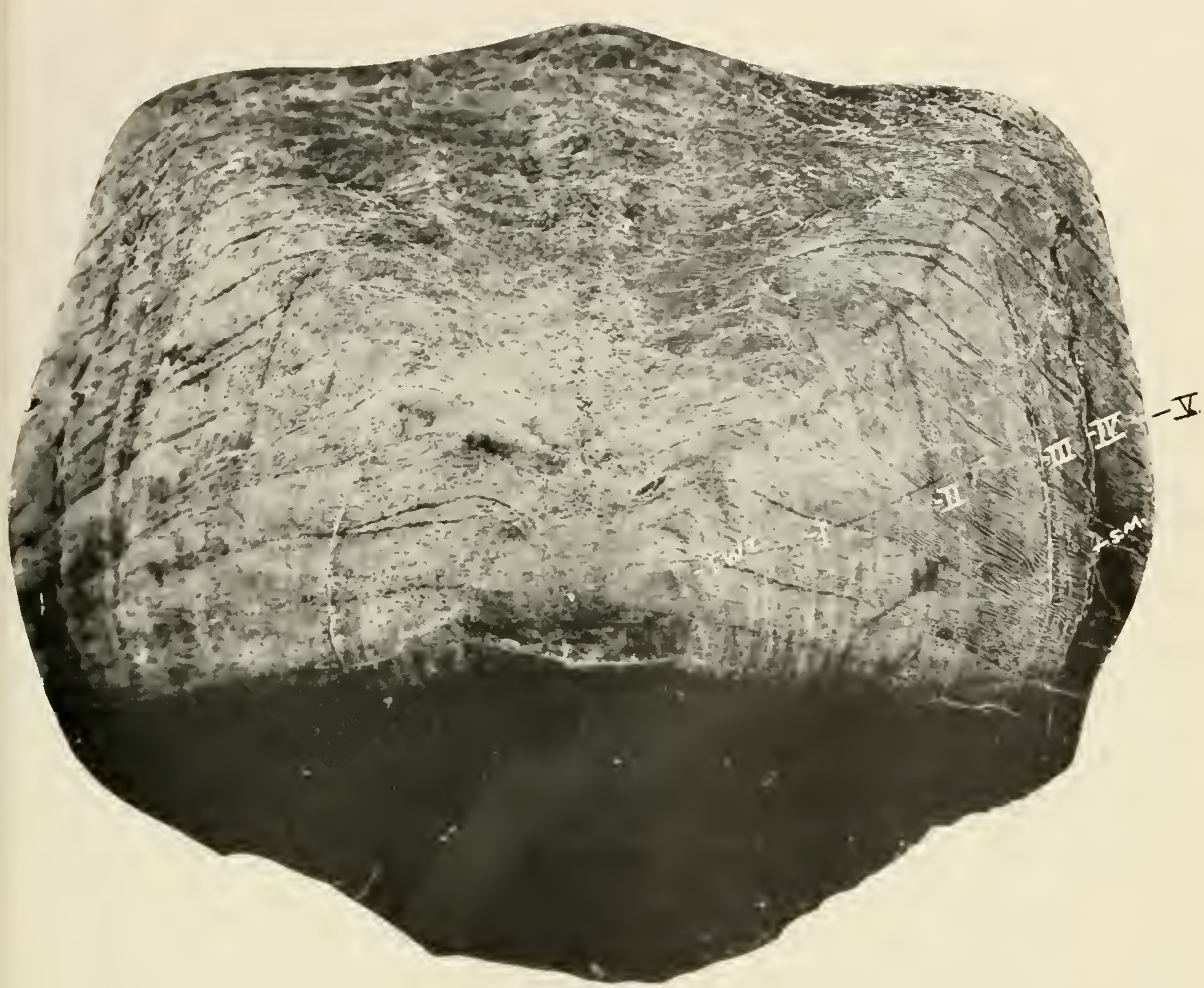


FIGURE 6.—Scale from a 19-inch female shad weighing 4 pounds. The single spawning mark (S. M.) is very clear on this particular scale. Note that the fourth transverse groove is branched. The Roman numerals indicate annuli and spawning mark.

A Recordak projector, designed for microfilm reading, and a binocular microscope of low power were tried as sources of magnification. The Recordak projector was found to be satisfactory for projecting and reading the easily read scales, but where difficulties occurred, it was found that the microscope gave a better image of the scale markings, especially of the spawning marks. Most of the impressions were read by the latter method. The illustrations used in this paper are negatives made from the image on the ground-glass screen of the Recordak projector.

An attempt was made to read 400 selected scales by the conventional method of counting annuli and spawning marks. Agreement in both reading and between 2 independent readings by 2 persons was obtained on 164, or 41 percent of the scales. Agreement between independent readings by two persons on the other 236 scale samples was poor because of poorly defined annuli and numerous false annuli. Because of this high percentage of disagreement it was considered necessary to develop criteria to distinguish the true from the false annuli or otherwise indicate the true age of the fish.

CRITERIA FOR DETERMINING AGE

Counting transverse grooves

Only those 164 scales that were clearly marked and on which consistent agreement had been

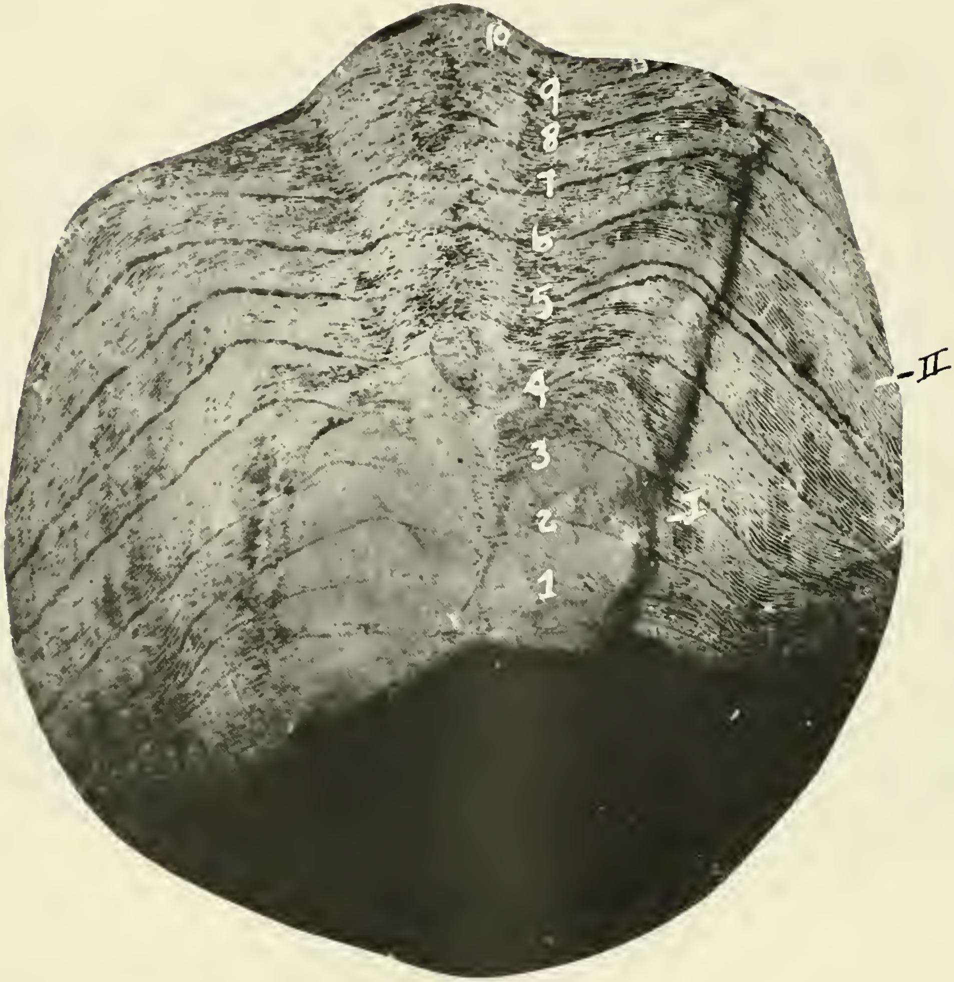


FIGURE 7.—Scale from a small male shad. Note that there are 10 transverse grooves to the edge of the scale as indicated by Arabic numerals. The second annulus is just within the periphery of the scale, and was formed during the winter just previous to this migration into fresh water where the fish was caught.

reached were used in the attempt to develop criteria for age analysis. Borodin's (1925) method of age determination by transverse grooves was tried. However, he gave no clear definition of what constitutes a complete or incomplete transverse groove; since none that we could devise appeared to give the desired results, this method was discarded.

While trying Borodin's method on the clearly marked scales, we noticed that the number of transverse grooves entering the fresh-water zone, and also the first, second, and third annuli, were almost constant from fish to fish. It was also observed that the spacing between transverse grooves, as with annuli, was proportional to growth. In other words, the distance between grooves becomes proportionally less as the fish grows older and its growth slows. Since the formation of grooves seemed to be a function of age and growth, it appeared that their numbers might be used as an index to the amount of growth taking place in any period and to locate the true annuli on scales that were confused by false annuli.

To check these observations, counts were made of the number of transverse grooves entering the fresh-water zone, first, second, and third annuli on the 164 easily read scales. Counting began with the first transverse grooves above the baseline, and grooves which branched were counted as one only. All the transverse grooves entering the fresh-water zone from one side were counted, including those that just touched the line enclosing the fresh-water zone. Those counted included incomplete grooves (not joined in the middle of the scale) as

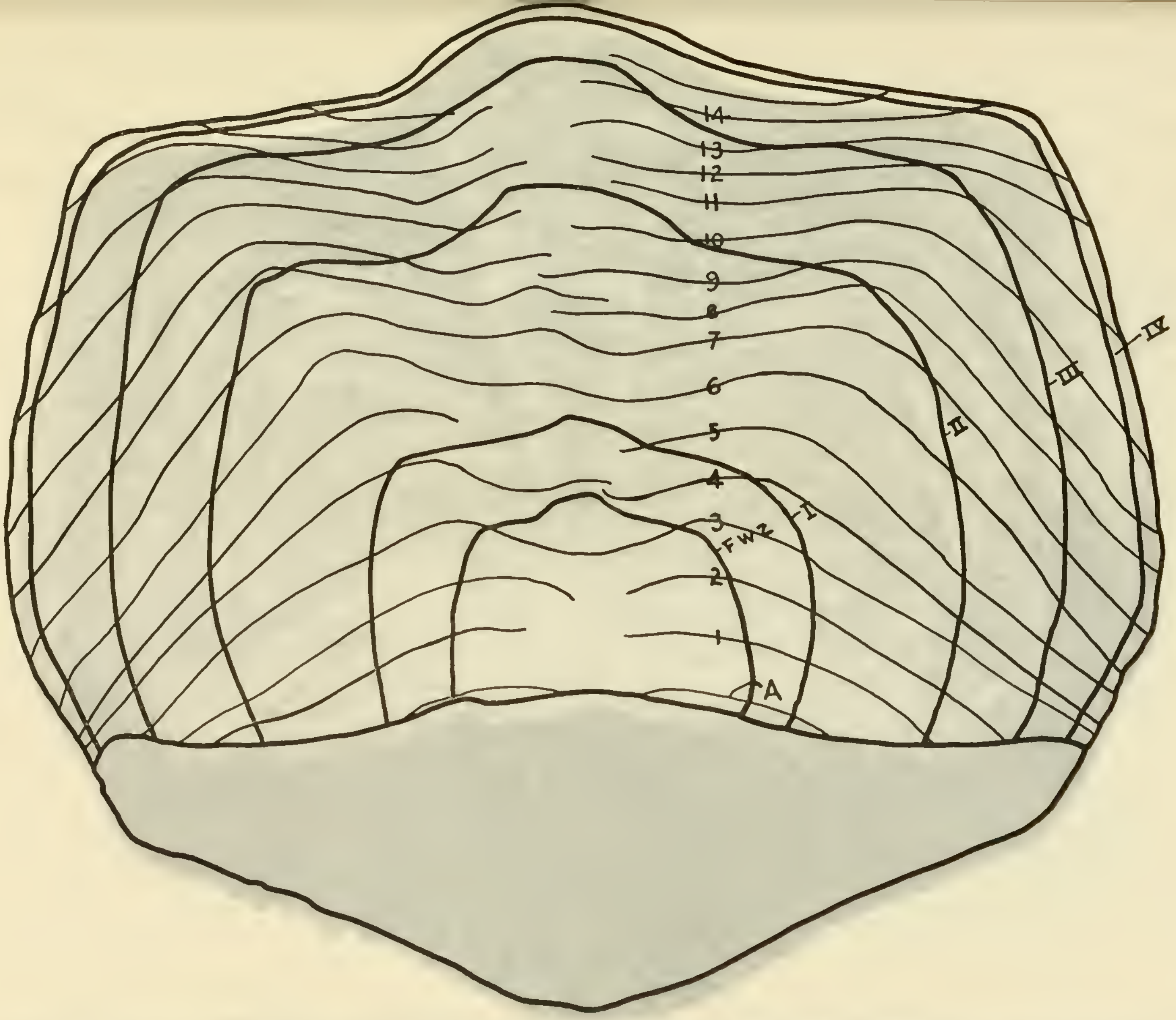
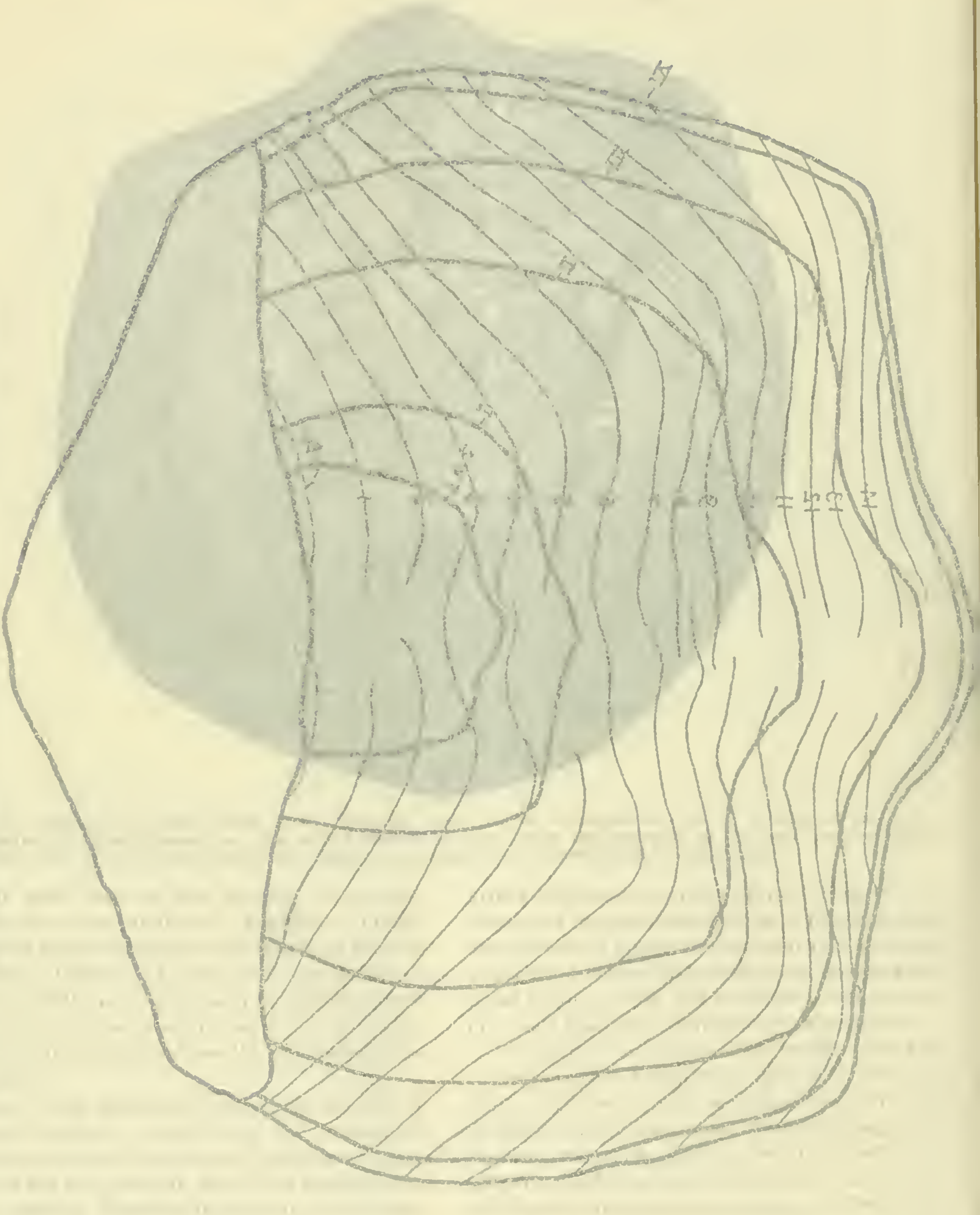


FIGURE 8-A.—Overlay to emphasize the major features of the shad scale in figure 8.



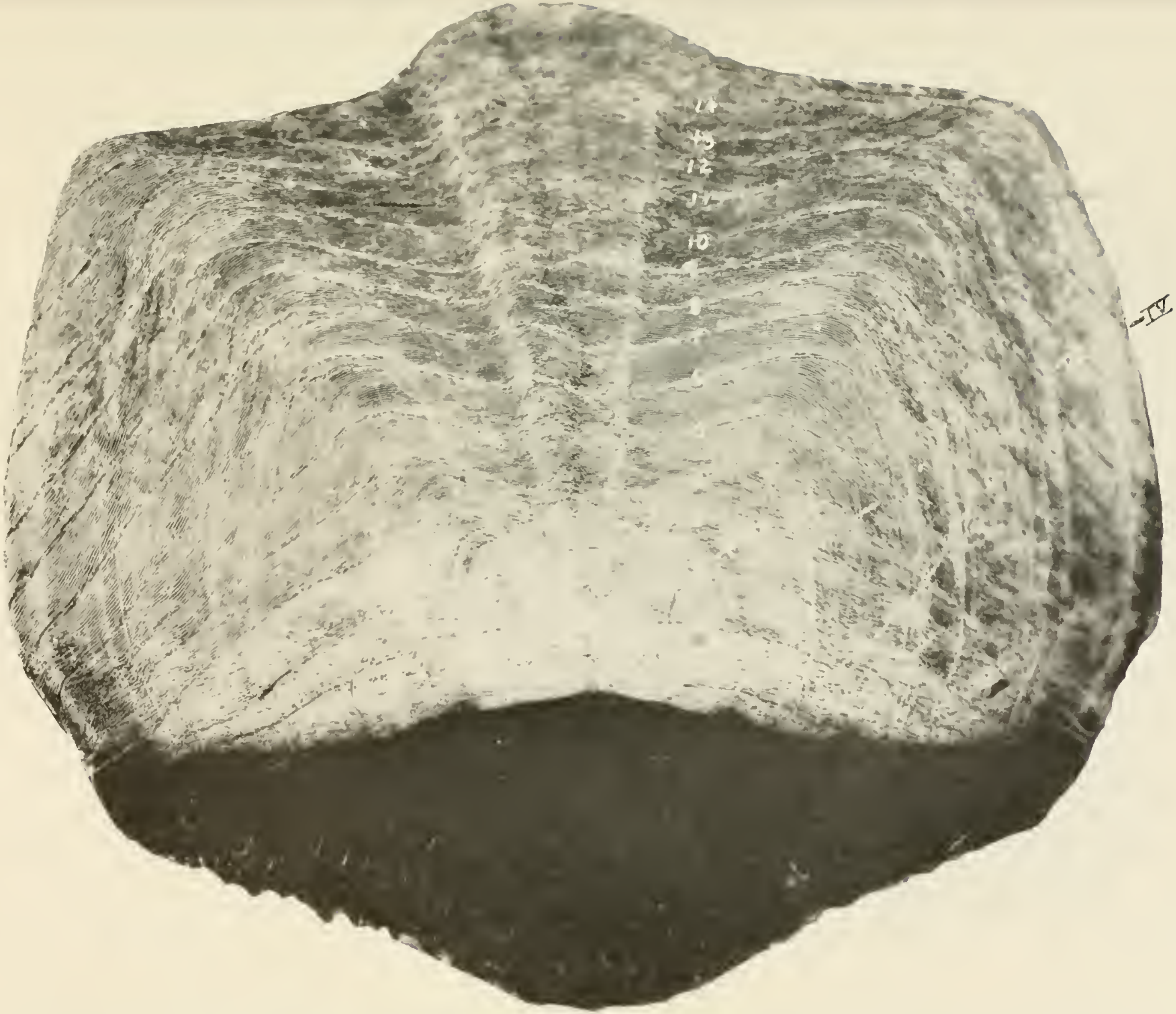


FIGURE 8.—Scale from a female shad measuring 18.7 inches and weighing 4 pounds. Arabic numerals indicate transverse grooves, *A* the base line, Roman numerals the annuli, and *FWZ* the fresh-water zone. Note the annulus just inside the periphery of the scale which was laid down during the winter just previous to spawning.

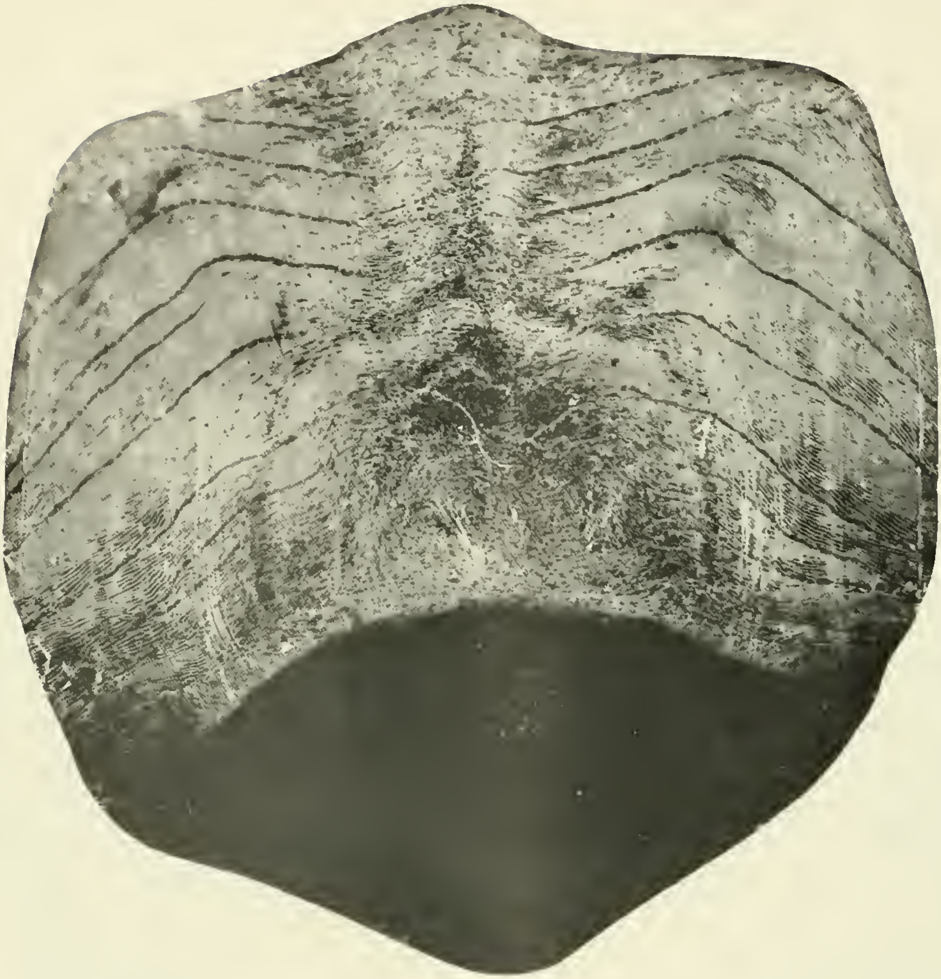


FIGURE 9.—Scale from a male shad that was probably 2 years old. This figure illustrates the appearance of a regenerate scale.

well as complete grooves (extending unbroken from one edge to the other). Figure 8 illustrates this procedure of counting by numbering the transverse grooves 1, 2, 3, and so on, starting with the first transverse groove above the baseline. Since it is impossible to obtain photographs of shad scales with all details clearly shown, the diagrammatic overlay of figure 8 was prepared to help illustrate the items discussed. These are seen while actually reading the scales by changing the focus of the microscope to bring out each detail. The scale in this figure is from a 4-year-old female taken during its first spawning migration. On this scale there are 3 transverse grooves lying within the fresh-water zone, 5 within the first annulus, 10 within the second annulus, and 14 within the third annulus.

The transverse-groove counts made on the 164 scales are shown in table 1. The number of transverse grooves lying within the fresh-water zone of the scale ranges from 1 to 5, but is usually 2 or 3. The number entering the area enclosed by the first annulus ranges from 4 to 7, but is usually 5 or 6. Within the second annulus, counts of 9 and 10 transverse grooves predominate, but the range is from 8 to 11. The number entering the area enclosed by the third annulus is generally 13 or 14, with a range from 12 to 16. On a few fish which had not spawned until they were 5 years old or older, it was found that 16 to 18 transverse grooves came into the area enclosed by the fourth annulus; but, because of the confusion of lines caused by the scarred area in the central anterior portion of most scales, it was found to be of value to use groove counts beyond the third annulus. This is not a handicap, however, because the annuli beyond the third are usually legible.

TABLE I.—*Frequency distributions of number of transverse grooves entering area enclosed by fresh-water zone and first, second, and third annuli on scales of 164 shad taken in the Hudson River, spring 1950*

Number of transverse grooves	Distribution of 164 counts in—							
	Fresh-water zone		First annulus		Second annulus		Third annulus	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	7	4.3						
2	63	38.4						
3	81	49.4						
4	12	7.3	6	3.7				
5	1	.6	85	51.8				
6			69	42.1				
7			4	2.4				
8					16	9.8		
9					58	35.4		
10					78	47.5		
11					12	7.3		
12							8	4.9
13							57	34.8
14							79	48.2
15							18	10.9
16							2	1.2
Total	164	100.0	164	100.0	164	100.0	164	100.0

Constancy of transverse-groove counts

To determine if the numbers of transverse grooves were constant within the various annuli on scales taken from various locations on the fish, selected samples of scales were mounted and read from five predetermined body locations on each of 26 Hudson River shad brought to the laboratory for special studies. The five locations chosen on the left side of each shad were as follows: (1) The midline of side just behind the gill opening; (2) the midline of side under the dorsal fin; (3) the midline of side near the tail; (4) just under the dorsal fin; (5) just above the pelvic fins. A count of the number of transverse grooves entering the fresh-water zone and each of the first 3 annuli was made from a scale from each of the 5 locations. This procedure was repeated for each of the 26 shad. In most cases we found no variation in transverse-groove counts between scales from the five locations on individual fish, and at most they varied not more than ±1. The slight variation in scales from different locations could be a result of the difference in legibility of markings and of possible error in counting, but in all cases the counts fell within the ranges shown in table 1.

It should be pointed out that the most symmetrical and legible, and therefore most easily read scales, are located on the midline of the side below the dorsal fin. Since even in this location many are regenerated scales (fig. 9), it was found necessary when sampling in the field to take about 20 scales in order to be sure of 2 good ones for mounting.

Spawning-mark criteria

The transverse grooves cannot be seen clearly on the part of the scale beyond the first spawning mark, due to scarring of the scale surface and the closeness of the spawning marks to each other. Since the spawning marks in most cases are clearly visible, there is no need for any index to them, for usually after a shad has spawned once, the spawning marks on the scales can be used with the annuli to determine the age of the fish. Only on shad that have spawned many times do the spawning marks become so crowded near the edge of the scale that they are hard to separate. This situation may be observed in figures 1 and 10 which show five spawning marks each. As many as nine spawning marks have been found on scales of individual fish taken in the 1950 Hudson River sample. On these scales it is usually possible to find traces of each spawning mark clearly visible just below the baseline in the posterior field of the scales where apparently not so much absorption takes place as in the anterior field.

Another problem encountered with spawning marks is that during the first spawning migration the previous year's scale growth around the periphery of the anterior portion is sometimes partially or wholly eliminated.

It is important when reading shad scales to examine the spawning marks to determine if an annulus has been eroded away. On scales where the annulus, laid down a year previous to the first spawning, has disappeared in the anterior portion of the scale due to erosion, a part of the annulus may be found near or just below the baseline of the scale inside the spawning mark, indicating that the absorption process does not affect the posterior portion of the scale to the same extent as the anterior portion. Figure 11 illustrates such a situation, and in reading this scale the part of the annulus remaining in the posterior region and the

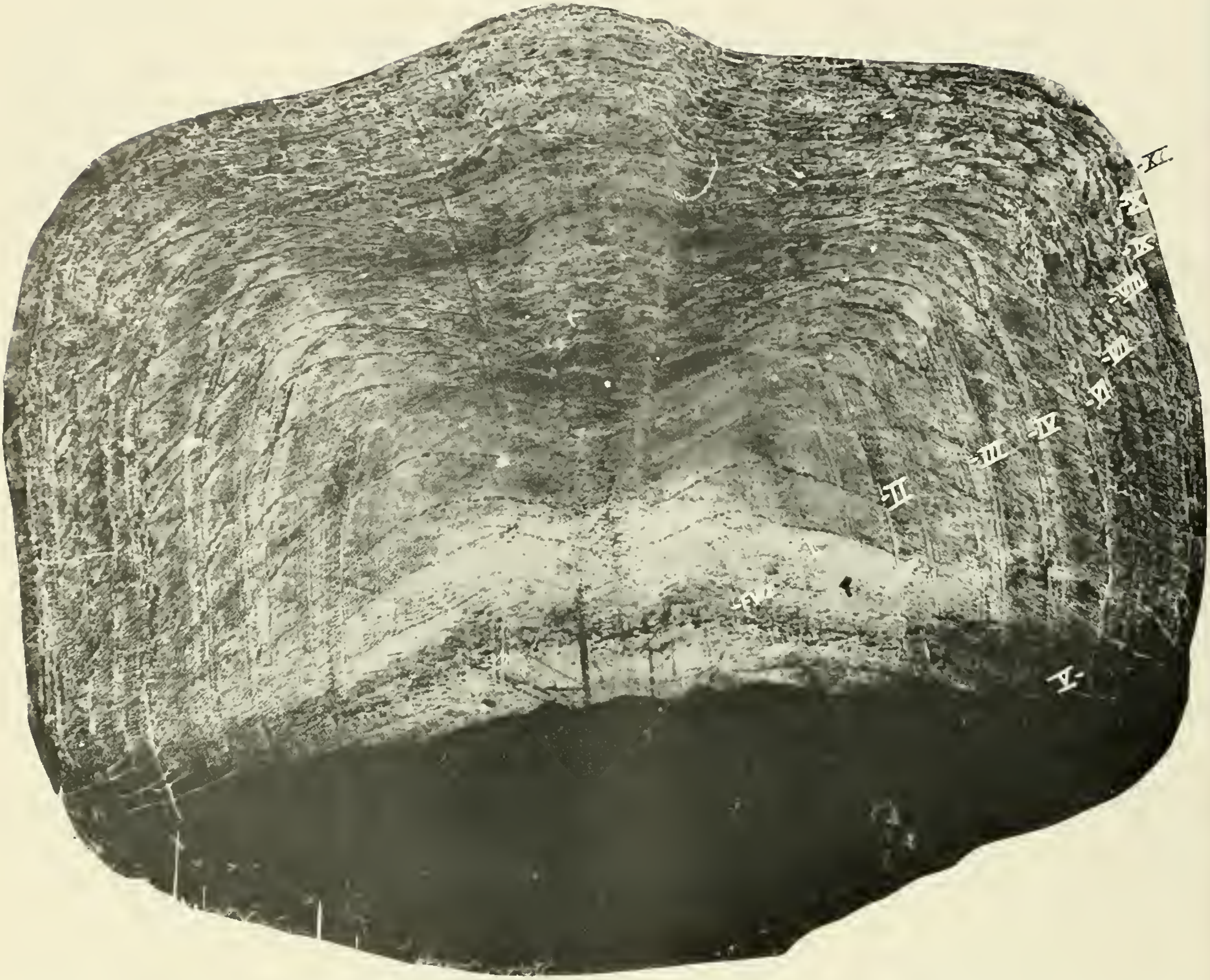


FIGURE 10.—Scale from an unusually large shad, a female, measuring 22.7 inches and weighing 7 pounds 9 ounces. Roman numerals VI through X represent spawning marks. Unfortunately, in this illustration the posterior portion of the scale is obscured so that the fifth annulus cannot be seen as separate from the first spawning mark just below the baseline in the posterior portion.

spawning mark should each be counted as a year. We were fortunate in obtaining, through our tagging program in the Connecticut River during 1951, direct evidence of the amount of absorption occurring while the shad is in fresh water. Shown in figure 12 is a scale taken from a shad at the mouth of the Connecticut River during a tagging operation: it shows five distinct annuli and a space to the edge of the scale representing the growth during the sixth year. This shad was just entering the river on its migration to the spawning grounds as is evidenced by the smooth scale margin. A scale was taken from this same tagged fish when it was caught 51 days later off the coast of Massachusetts by a trawler: this fish apparently had spawned in the Connecticut River and then migrated out of the river and northward into the Atlantic Ocean. The second scale is shown in figure 11. One year's growth has almost been eroded away, leaving only pieces of the fifth annulus to be seen around the anterior periphery of the scale. The fifth annulus can still be clearly seen near the baseline just inside the ragged edge of the scale.

The amount of erosion, or absorption, during the first spawning migration appears to vary with the age at first spawning. For example, the scale of a shad spawning for the first time at 6 years

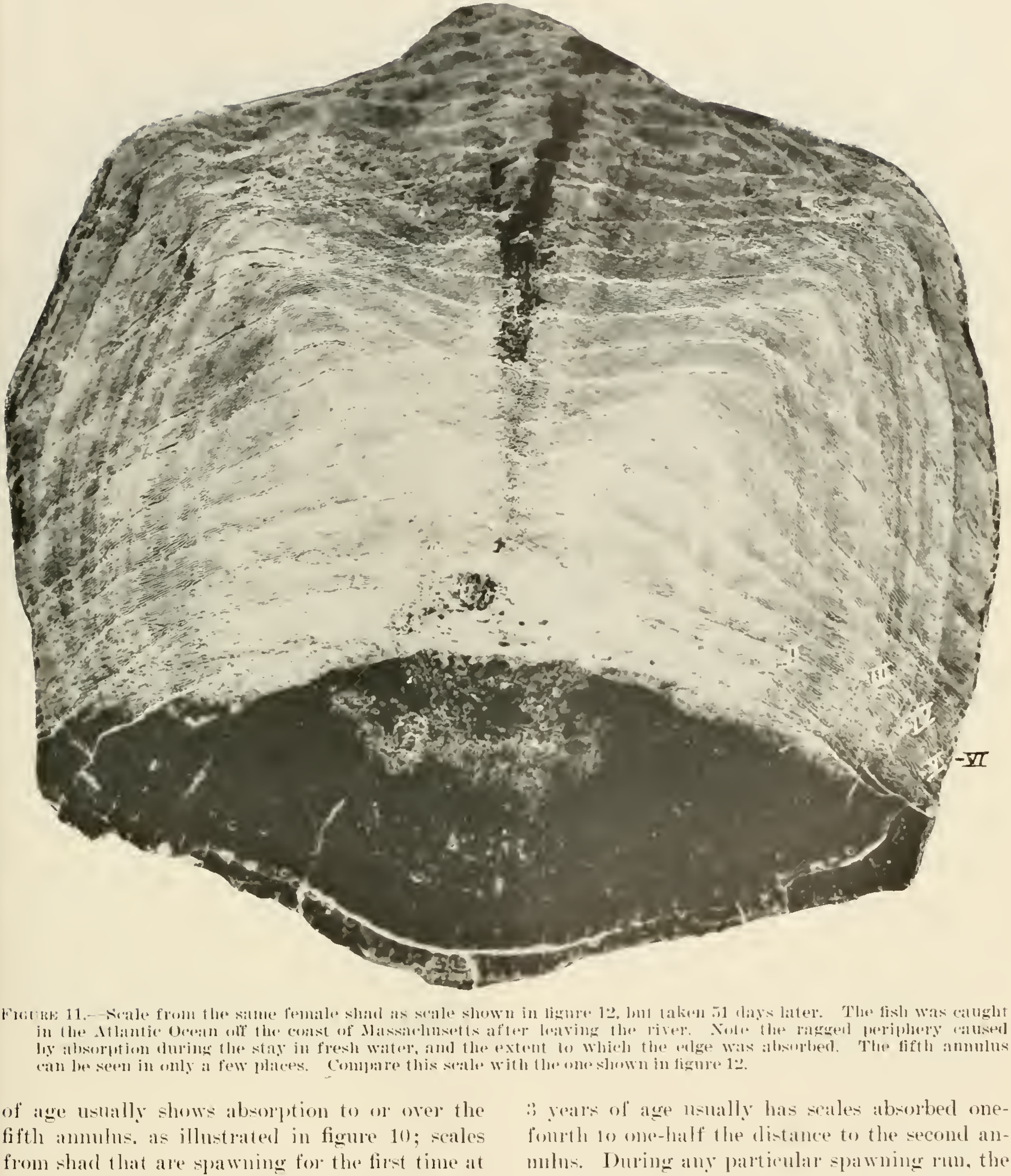


FIGURE 11.—Scale from the same female shad as scale shown in figure 12, but taken 51 days later. The fish was caught in the Atlantic Ocean off the coast of Massachusetts after leaving the river. Note the ragged periphery caused by absorption during the stay in fresh water, and the extent to which the edge was absorbed. The fifth annulus can be seen in only a few places. Compare this scale with the one shown in figure 12.

of age usually shows absorption to or over the fifth annulus, as illustrated in figure 10; scales from shad that are spawning for the first time at 5 years of age are usually absorbed back to the fourth annulus; scales from shad spawning for the first time at 4 years are usually absorbed back about half way toward the third annulus as shown in figure 6; and a shad coming back to spawn at 3 years of age usually has scales absorbed one-fourth to one-half the distance to the second annulus. During any particular spawning run, the amount of absorption depends on the time the fish spends in fresh water. If the scales are from shad taken just before they enter fresh water, little or no absorption of the previous year's growth should be found.

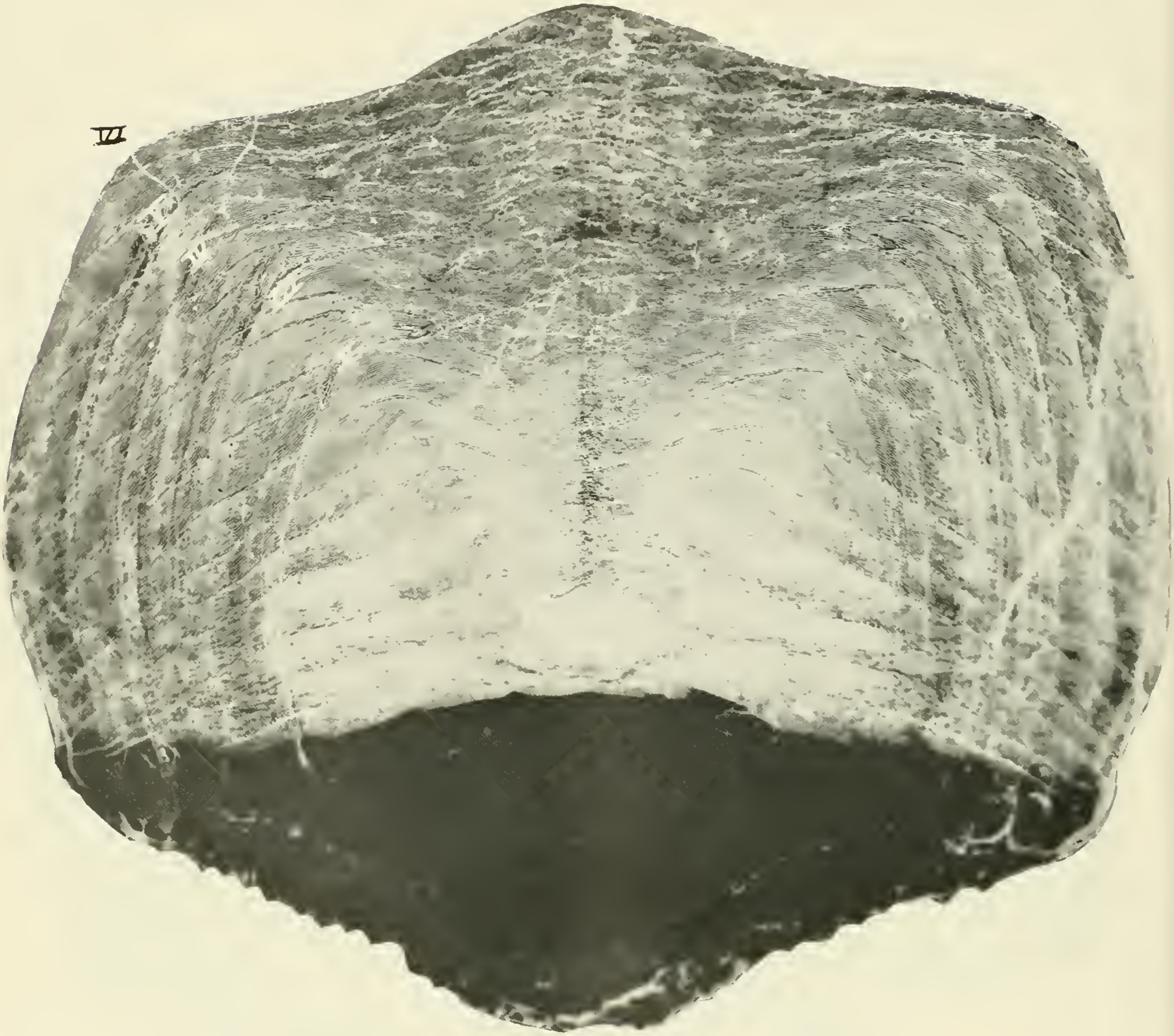


FIGURE 12.—Scale from a 6-year-old female shad measuring 19.1 inches. The fish was taken at the mouth of the Connecticut River on its way to spawn for the first time.

APPLICATION OF CRITERIA

The criteria, as described, were applied to the scales on which poor agreement was reached, and little difficulty was experienced in determining the location of the first, second, and third annuli. Once the location of an annulus was determined by groove count, the annulus usually could be traced from the anterior sculptured area into the posterior area of the scale even though obscured and confused by false annuli. Usually the true annuli were represented by more heavily defined ridges in the posterior section than the false annuli.

The fourth, fifth, and sixth annuli were usually clearly visible and proportionately spaced on scales of fish which had not previously spawned; hence, by using transverse-groove counts to locate the first, second, and third annuli and then counting each annulus past the third one, it was possible to determine the age of shad which had not previously spawned.

Proficiency in interpreting the age of any species of fish from scales requires practice. This is especially true when working with scales as difficult to read as the shad's; however, it is believed that by applying the criteria presented here, anyone wishing to learn to read shad scales accurately can do so in a relatively short time. It is suggested that anyone interested in applying these criteria should select several hundred shad scales, and read them a number of times until the different readings reach a desired level of agreement.

SUMMARY

From scales of the Atlantic shad (*Alosa sapidissima*) collected in the Hudson River in the spring of 1950, 164 of the more easily read scales were selected to serve as the basis for establishing criteria for determining the age of shad from their scales.

By counting the number of transverse grooves entering the fresh-water zone, and the first, second, and third annuli, it was found that the number of such grooves is relatively constant from fish to fish. The predominant number of transverse grooves entering the fresh-water zone was 3; the first annulus, 5; the second annulus, 10; and the third annulus, 14. In a period of slow growth when two annuli lay close together, the distance between the transverse grooves was found to be proportionately less. Once the location of an annulus was determined by groove count, the annulus usually could be traced.

When a shad has previously spawned the spawning marks must be used with the annuli to determine the age of the fish. The spawning marks are scarlike rings extending around the anterior portion of the scale which are caused by erosion or absorption of the scale when the shad enters fresh water to spawn. The amount of absorption that occurs depends on the age of the fish at the time it makes its first spawning migration. Thus, it was found that scale absorption on a fish making its first spawning migration when 3 years old usually extends from one-fourth to one-half the distance to the second annulus. On a scale from a 6-year-old shad spawning for the first time, however, the absorption usually extends to or over the fifth annulus. It is important, therefore, to examine scales closely from fish apparently spawning for the first time at 5 or 6 years of age to determine if an annulus has been absorbed during the first spawning migration. Usually, remnants of the annulus previous to the first spawning can be seen near the edge of the posterior region of the scale. When there are several spawning marks on a scale, and the marks have overlapped each other, traces of each spawning mark are clearly seen just posterior to the baseline.

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POPULATION HETEROGENEITY IN THE PACIFIC PILCHARD

By Frances E. Felin

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POPULATION HETEROGENEITY IN THE PACIFIC PILCHARD

By Frances E. Felin, *Fishery Research Biologist*

In the course of routine examination of scales of the Pacific pilchard (*Sardinops caerulea*) several investigators working together had for a long time noticed the consistent occurrence of distinctively small individuals among the 5-year olds. This suggested the possibility that this species might be composed of more than one population, each having common and genetically distinct attributes. One of these attributes appeared to be growth rate; others might include habits, distribution, anatomy, and physiology. Possibly also these populations would have differing rates of birth and death. If this hypothesis should prove true, then the characteristics of each population must be taken into account in any study involving population dynamics.

To examine the proposition that the species *Sardinops caerulea* is a complex of different populations, distinguishable by peculiarities in growth rate, we undertook an intensive study of the growth characteristics as recorded on pilchard scales, and we analyzed these data in the light of certain pertinent vital statistics. The following paper is a report of that study.

The materials for this study are scales, and age and length data from pilchard sampled by State and Federal agencies. These were collected in as nearly random a fashion as possible from the catches at major ports along the Pacific coast where fishing was carried on during each fishing season from 1941–42 through 1949–50. Since validation of scale-reading techniques for Pacific pilchard (Walford and Mosher 1943a and 1943b), the age and length composition of these samples have provided the vital statistics from which may be estimated the annual accrual to the stocks by recruitment and growth, and the losses due to fishing and natural mortality and/or unavailability of fish to the fishery.

The assistance of the Fisheries Research Board of Canada, the Washington Department of Fisheries, the Oregon Fish Commission, the California Department of Fish and Game, and of the many persons who have made possible the continued cooperative program of sampling the catch, is gratefully acknowledged. I wish also to thank Dr. L. A. Walford, O. E. Sette, and J. C. Marr for their constructive criticism and encouragement; Dr. G. S. Myers, Stanford University, for his review of the manuscript; and T. M. Widrig for his assistance in preparing the statistical data.

AVERAGE GROWTH DATA

Growth curves of a given year class of pilchard may be constructed from the mean observed lengths of that year class in successive seasons (Phillips 1948). Such growth curves fluctuate in level from year to year because of the differential migration of the fish of different size (Clark and Janssen 1945) and age, and because of within-season and between-season variations in distribution of the population. Observed lengths, however, provide a useful check on back calculations of lengths, which are based on the proportionality of growth of scale to growth of fish.

DETERMINING LENGTHS BY THE DIRECT-PROPORTION METHOD

For calculating lengths of pilchard a direct proportionality is tentatively assumed in this study, so that

$$\frac{l_n}{l_t}=\frac{s_n}{s_t}$$

where l is length of fish, s is length of scale, n represents any given age, or annual ring on the scale, and t is total length of fish or scale. The scale, of course, is not formed when the fish is 0 mm. long. The extrapolated curve of the linear regression of fish length on scale length may show for adult fish of a given year class, a positive, a zero, or a negative y-intercept and since the scale cannot be laid down at a minus length of fish, the absolute value of the y-intercept can not be said to have a biological meaning. Regressions of pilchard length on scale length appear to be satisfactorily described by a linear equation over the range of ages 1- through 5-ring (Landa 1950). When the y-intercept differs significantly from zero, the percentage error in estimated length introduced by the assumption of direct proportionality will, of course, decrease with increasing age.

A variety of factors renders the calculated growth for the first year of life, or to the first ring on the scale, only an approximation. The amount of the first growth increment differs geographically, which is partly explained by the northward shift of spawning as the season progresses. Spawning also continues for some length of time at a given locality. There is consequent inequality in duration of the initial period of growth, so that the length of the first year, from the time spawned until the formation of the first winter annulus, depends upon the place and date of spawning. The time periods represented by the l_1, thus are not entirely comparable with those represented by other growth increments (l_n). Furthermore, there is least clarity in appearance of the first ring on pilchard scales and greater difficulty in locating it than is found with subsequent annuli, so that less reliability is associated with the mean value of the first growth increment, $\bar{l}_1$.

Average observed lengths at each age of all the year classes sampled in the commercial catch over nine seasons in five regions along the Pacific coast are given in table 1. The means given for each age in each region were obtained by assigning equal weight to each year-class average. These means were then taken as representative of a mean curve of growth for each area of catch. (See also Phillips 1948, p. 7.)

TABLE 1.—*Average length of pilchard in the commercial catch of five Pacific-coast areas, by year class and age group*

Year class	1-ring		2-ring		3-ring		4-ring		5-ring		6-ring		7-ring	
	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length
British Columbia:		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
1934													40	245
1935											80	241	12	242
1936									237	236	51	244	39	250
1937							307	230	92	239	100	246	27	247
1938					142	216	104	230	148	239	93	245	45	250
1939			255	193	313	215	287	234	204	242	95	247	32	254
1940	10	175	84	204	89	226	117	239	67	245	26	250	30	253
1941					20	231								
1942			37	195	38	225	10	241	17	250				
1943	14	183	29	211			15	243						
Mean	24	179	405	201	602	223	840	236	765	242	445	246	225	249
Pacific Northwest:[1]														
1934													62	248
1935											112	242	12	242
1936									331	236	53	244	40	249
1937							483	229	95	239	104	245	27	247
1938					294	215	111	231	164	239	93	245	53	250
1939			680	191	390	215	322	233	204	242	122	249	61	255
1940	35	166	91	203	101	225	117	239	86	247	83	253		
1941	(*)				20	231	(*)		19	253				
1942	(*)		37	195	44	225	22	244						
1943	14	183	29	211	10	236								
1944	(*)													
Mean	49	174	837	200	859	224	1,055	235	899	243	567	246	255	248
San Francisco:														
1935											(*)		12	240
1936									44	220	86	231	33	241
1937							186	217	256	227	93	239	132	248
1938					862	209	736	222	348	232	403	244	28	253
1939			1,186	199	1,346	216	959	228	896	241	55	247	12	255
1940	21	180	205	208	574	223	665	236	78	240	(*)			
1941	(*)		51	206	185	223	80	222	(*)					
1942	48	173	313	212	191	222	16	238						
1943	46	182	147	210	13	234								
1944	(*)		14	209										
1915	18	168												
Mean	133	176	1,916	207	3,171	221	2,642	227	1,622	232	637	240	217	247

See footnotes at end of table.

TABLE 1.—*Average length of pilchard in the commercial catch of five Pacific-coast areas, by year class and age group*—Con.

Year class	1-ring		2-ring		3-ring		4-ring		5-ring		6-ring		7-ring	
	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Monterey:														
1935											(*)		11	232
1936									36	218	55	231	18	237
1937							164	215	161	229	98	235	44	245
1938					903	206	700	220	367	230	163	242	15	247
1939			2,487	195	1,684	214	1,167	226	537	239	58	247	16	254
1940	447	175	641	205	949	221	470	234	71	236	21	243		
1941	137	164	255	198	352	219	150	219	43	237				
1942	570	164	1,379	204	320	219	77	234						
1943	450	170	255	209	135	232								
1944	73	172	83	207										
1945	324	184												
Mean	2,001	172	5,100	203	4,343	218	2,728	225	1,215	232	395	240	104	243
San Pedro:														
1935											11	223		
1936									43	212	15	215		
1937							140	212	58	214	22	223		
1938					1,090	202	448	210	97	219	31	231		
1939			1,756	194	1,301	206	443	213	178	224	14	224		
1940	419	179	1,373	198	831	206	415	213	44	218	(*)			
1941	176	181	1,112	196	1,141	206	151	213	26	222	11	237		
1942	485	180	1,060	204	242	206	59	220	45	237	(*)			
1943	546	187	337	200	186	213	83	228	9	219	(*)			
1944	105	182	283	205	161	219	33	213	28	212				
1945	397	195	281	210	99	210	61	208						
1946	195	169	407	199	210	206								
1947	59	187	253	198										
1948	75	189												
Mean	2,757	183	6,862	200	5,264	208	1,833	214	528	220	104	226		

[1] Includes samples from waters off Washington and Oregon.
*Less than 10 fish sampled.

TRANSFORMATION OF GROWTH CURVES

When such growth curves of means-of-average observed lengths for each area are transformed, using Walford's (1946 a) plot of l_{n+1} on l_n, figure 1 results. These transformations show marked deviation from the linearity characteristic of this plot for more homogeneous groups of fish (or of other animals). They are illustrative, however, of growth characteristics of different areas. As defined by Walford, these are (1) the slope of the regression, k, representing the rate of deceleration of growth; and (2) the predicted ultimate size, $l_\infty = \frac{y\text{-intercept}}{1-k}$. Pilchard landed at Monterey and San Francisco show growth characteristics intermediate between those of catches landed in the south at San Pedro and in the Pacific Northwest off Oregon, Washington, and British Columbia.

Growth data on European pilchard (*Sardina pilchardus*) assembled from various sources by De Buen (1937) are plotted similarly (as transformations) in figure 2 for different geographical areas. These curves are based on back calculations of length obtained for the most part by the direct-proportion formula. Differing growth types, possibly representing clines (or gradients) of growth, are indicated from north to south, extending from waters off England through the southern European Atlantic to the Mediterranean. In figure 2, solid symbols represent transformations of growth curves of pilchard off Cornwall, Plymouth, and Northumberland; various crosses and parts of crosses show growth transformations of pilchard from the English Channel off Boulogne, from other waters south along the French and Spanish coasts as far as Cadiz and the Azores; and open symbols represent pilchard growth types from the Mediterranean. As early as 1913 Fage suggested, on the evidence of growth, that two distinct races of sardines exist, one in the Atlantic and another in the Mediterranean. He also noted (1920) that the relative dwarfism of Mediterranean races is not peculiar to the sardine, but has also been noticed in the anchovy and other species common to the two seas.

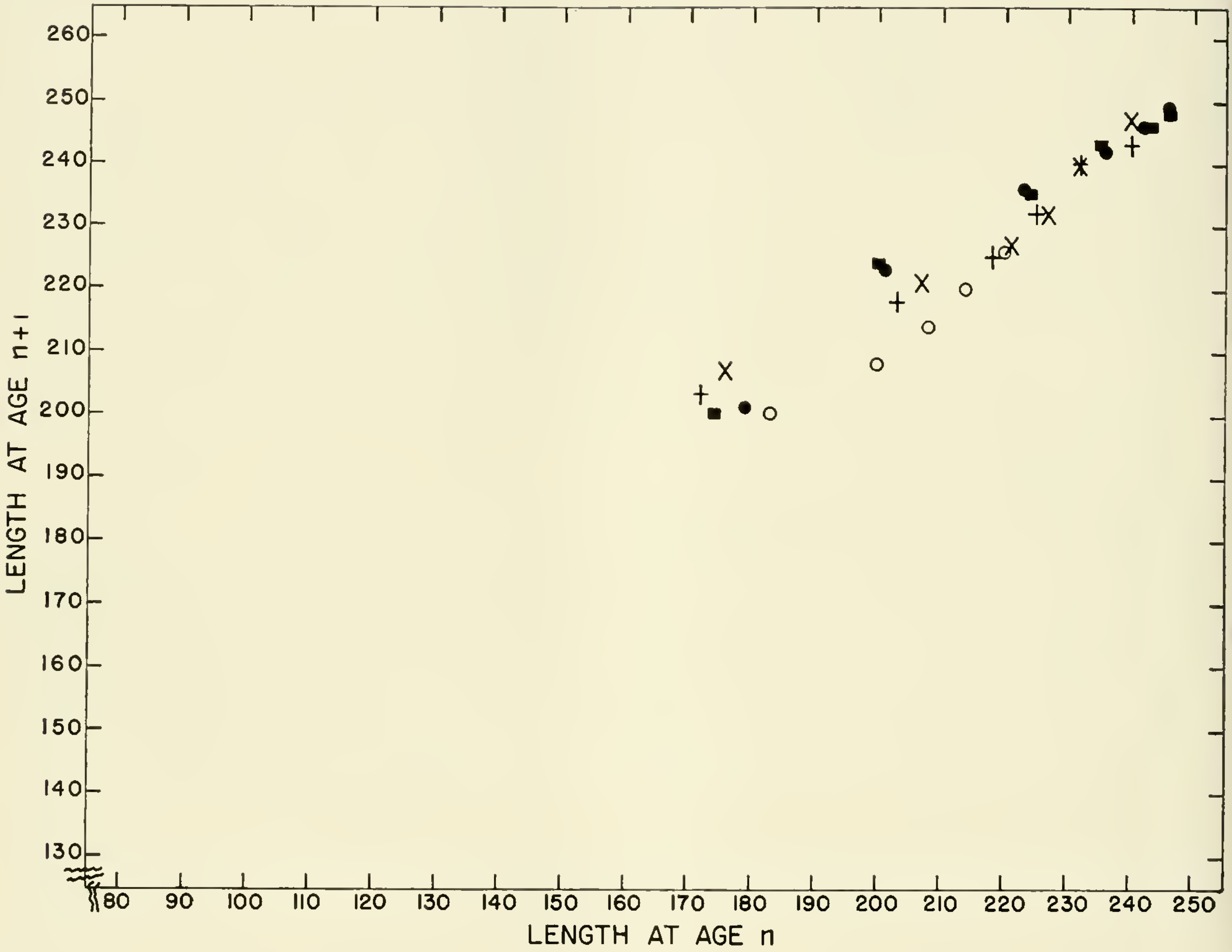

FIGURE 1.—Transformations of 9-season averages of observed lengths of Pacific pilchard at each age in five regions of catch. British Columbia averages represented by dot, Pacific Northwest by solid square, San Francisco by cross, Monterey by plus, San Pedro by circle.

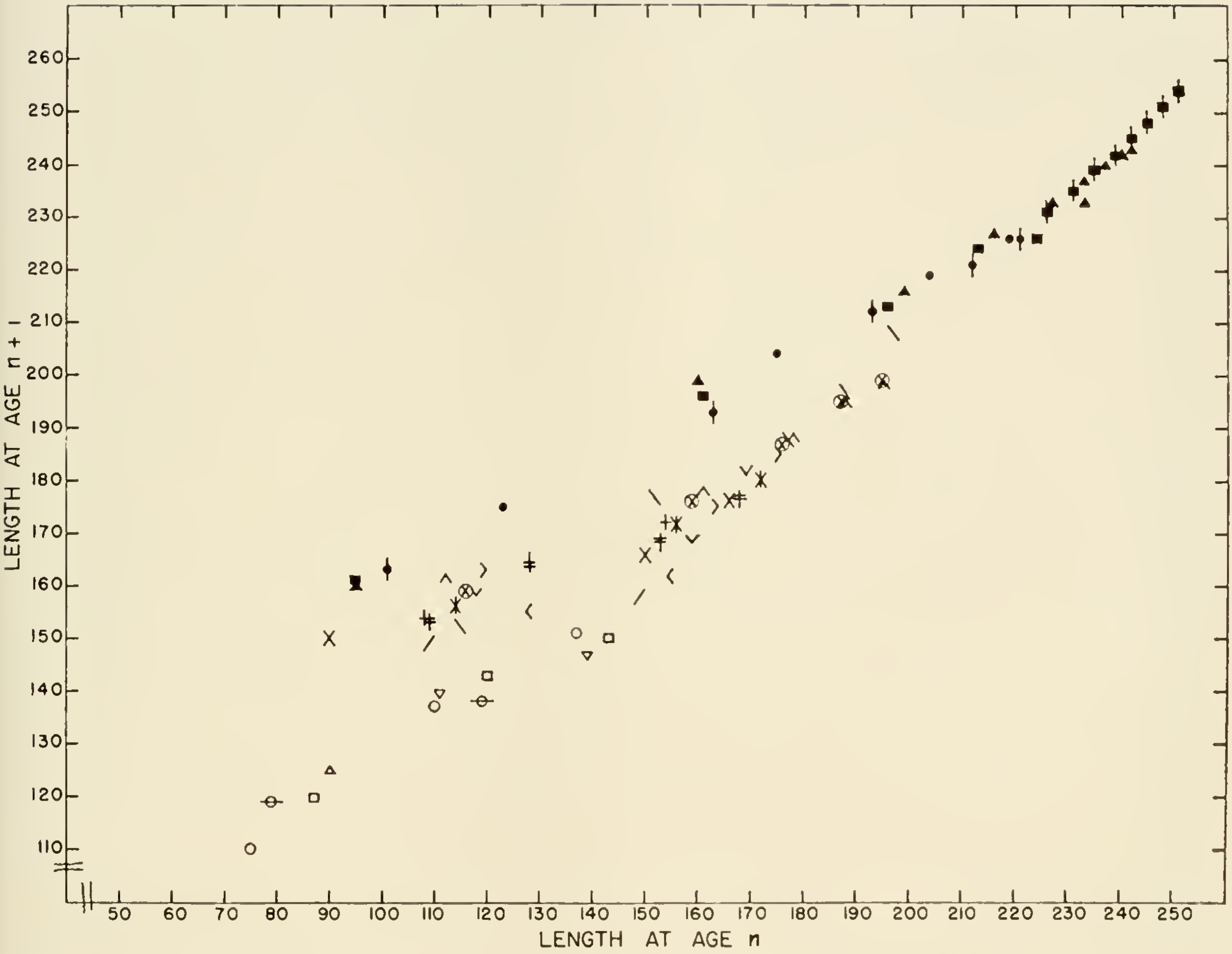

FIGURE 2.—Transformations of growth curves of European pilchard from different regions of catch. Solid symbols represent pilchard caught off England, various crosses and parts of crosses those off the French and Spanish coasts, open symbols those from the Mediterranean. (Data from De Buen 1937.)

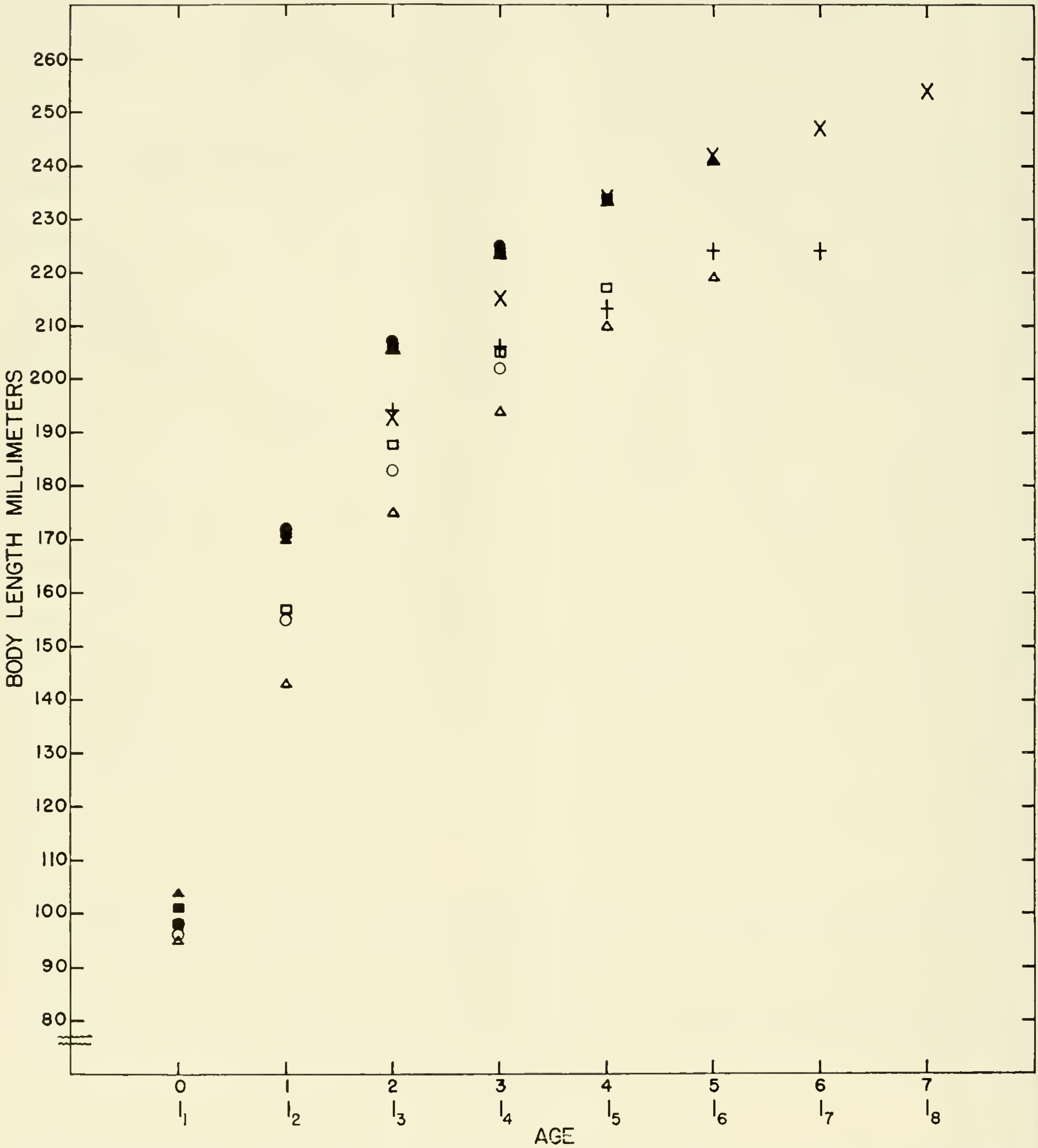

FIGURE 3.—Growth of pilchard of the 1939 year class taken in Canada and in San Pedro. Mean observed lengths of fish taken in Canada are shown by crosses, those in San Pedro by pluses. Mean calculated lengths of 4-, 5- and 6-ring fish are shown by circles, squares, and triangles, solid symbols for Canada, open symbols for San Pedro.

GROWTH CURVES OF 1939 YEAR CLASS

Utilizing mean calculated lengths (table 2) for a given year class of Pacific pilchard taken in the most northern region of catch, Canada, and in the most southern, San Pedro, we may compare growth curves derived from mean calculated lengths with those derived from mean observed lengths for each year class throughout its life in the fishery. An advantage in the transformation plot is graphically illustrated by figures 3 and 4. It is not readily apparent from the conventional growth curves of the 1939 year class (fig. 3) that the crosses delineating the growth curves derived from mean observed lengths of the year class in successive seasons express the same rate of deceleration of growth as do the mean back calculations of length for 4-ring, 5-ring and 6-ring fish (circles, squares, and triangles) of this 1939 year class. Solid symbols represent northern calculated-length data, open symbols the southern. These same curves transformed (fig. 4) show the relative constancy of slope (k) as well as level (y-intercept) of the regressions for northern and southern populations, whether plotted from observed or calculated length data.

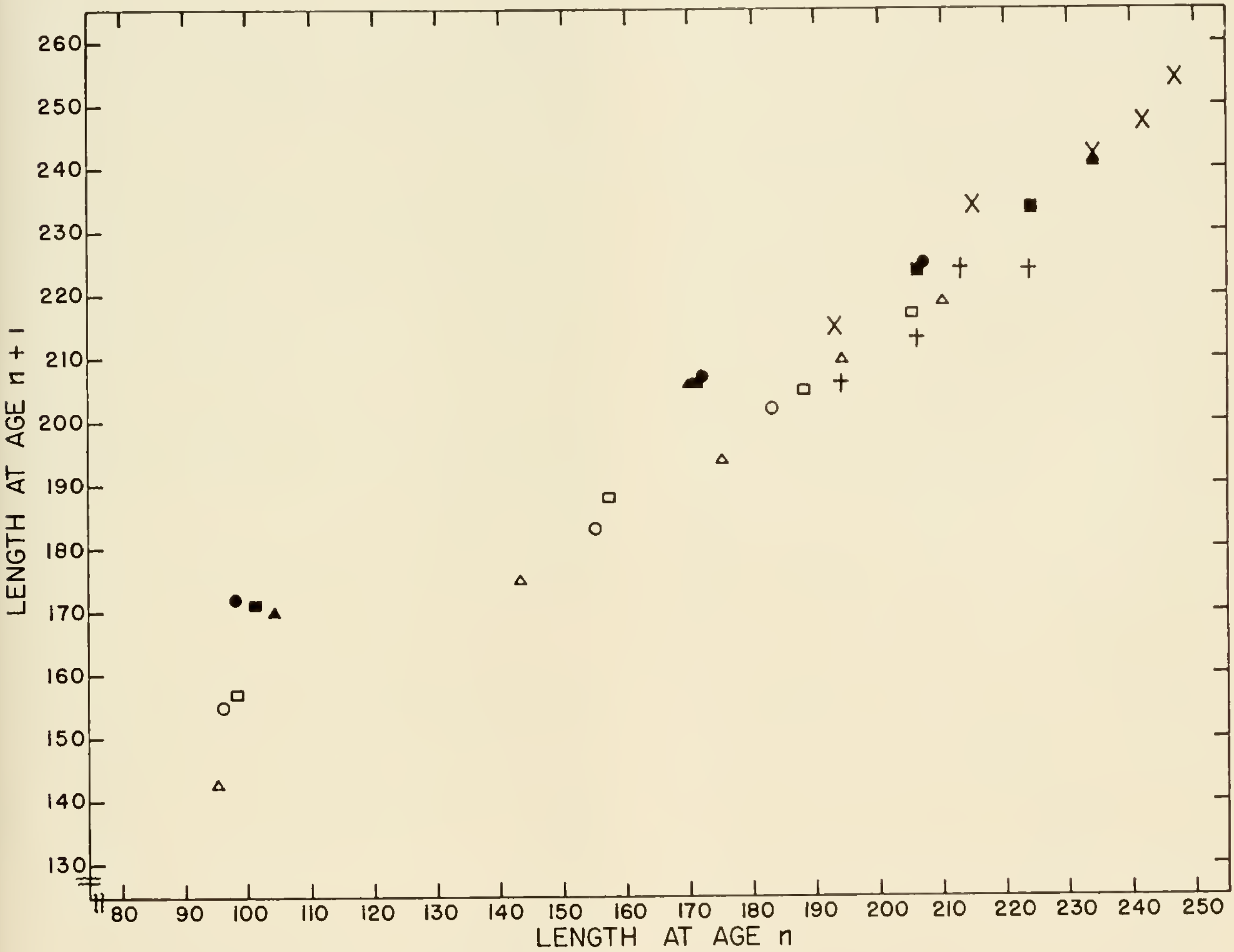

FIGURE 4.—Transformations of the growth curves of the 1939 year class shown in figure 3.

TABLE 2.—*Average calculated lengths ($\bar{l}$) of year classes at 4-ring and older, sampled in the commercial catch of pilchard, British Columbia and San Pedro*

[Parentheses indicate average based on 13 5-ring fish from Washington brackets, fish from Oregon; asterisks, 9 fish sampled]

Year class and calculated length ($\bar{l}$)	British Columbia			San Pedro		
	4-ring	5-ring	6-ring	4-ring	5-ring	6-ring
1937:						
$\bar{l}_1$	118	113	112	105	102	109
$\bar{l}_2$	175	173	172	161	156	161
$\bar{l}_3$	206	208	205	192	184	187
$\bar{l}_4$	223	225	223	205	197	202
$\bar{l}_5$	---------	236	234	---------	207	211
$\bar{l}_6$	---------	---------	241	---------	---------	218
1938:						
$\bar{l}_1$	103	107	110	96	98	103
$\bar{l}_2$	169	173	172	162	161	161
$\bar{l}_3$	203	206	205	188	188	191
$\bar{l}_4$	218	222	222	201	201	208
$\bar{l}_5$	---------	232	233	---------	211	217
$\bar{l}_6$	---------	---------	240	---------	---------	225
1939:						
$\bar{l}_1$	98	101	104	96	98	95
$\bar{l}_2$	172	171	170	155	157	143
$\bar{l}_3$	207	206	206	183	188	175
$\bar{l}_4$	225	224	224	202	205	194
$\bar{l}_5$	---------	234	234	---------	217	210
$\bar{l}_6$	---------	---------	241	---------	---------	219
1940:						
$\bar{l}_1$	108	112	112	103	105	---------
$\bar{l}_2$	179	178	182	156	158	---------
$\bar{l}_3$	213	211	211	185	184	---------
$\bar{l}_4$	230	228	227	202	200	---------
$\bar{l}_5$	---------	238	238	---------	211	---------
$\bar{l}_6$	---------	---------	246	---------	---------	---------
1941:						
$\bar{l}_1$	---------	(116)	[112]	100	107	---------
$\bar{l}_2$	---------	(186)	[179]	156	166	---------
$\bar{l}_3$	---------	(219)	[214]	187	195	---------
$\bar{l}_4$	---------	(236)	[231]	204	207	---------
$\bar{l}_5$	---------	(248)	[241]	---------	216	---------
$\bar{l}_6$	---------	---------	[248]	---------	---------	---------
1942:						
$\bar{l}_1$	107	95	[108]	116	109	---------
$\bar{l}_2$	183	166	[170]	174	170	---------
$\bar{l}_3$	213	211	[208]	198	203	---------
$\bar{l}_4$	232	231	[230]	211	219	---------
$\bar{l}_5$	---------	242	[244]	---------	230	---------
$\bar{l}_6$	---------	---------	[254]	---------	---------	---------
1943:						
$\bar{l}_1$	111	[112]	---------	115	*116	---------
$\bar{l}_2$	172	[177]	---------	174	*163	---------
$\bar{l}_3$	205	[213]	---------	203	*190	---------
$\bar{l}_4$	229	[234]	---------	218	*202	---------
$\bar{l}_5$	---------	[247]	---------	---------	*211	---------
1944:						
$\bar{l}_1$	[129]	---------	---------	133	130	---------
$\bar{l}_2$	[196]	---------	---------	175	169	---------
$\bar{l}_3$	[228]	---------	---------	193	185	---------
$\bar{l}_4$	[246]	---------	---------	205	197	---------
$\bar{l}_5$	---------	---------	---------	---------	207	---------

CONSISTENCY OF GROWTH CURVES

Year classes 1937 through 1942 provide sufficient data for construction of curves of growth similar to those of the 1939 class (see tables 1 and 2). For the year classes 1937 through 1940, the estimates of means have greater reliability owing to more extensive sampling during seasons 1941–42 through 1944–45. A decline in catches coincided with curtailment of the sampling program so that from seasons 1945–46 through 1949–50 the estimates of mean lengths are based on fewer fish.

The transformations for year classes 1937, 1938, 1940, 1941, and 1942 are similar in growth characteristics to those of the 1939 year class (see table 3). From analysis of covariance, no significant difference was apparent in the mean slopes, *k*, of the transformations between each of these year classes in the two areas of catch, Canada and San Pedro. That slope, or rate of deceleration of growth, is the more stable of the two growth characteristics, and that, with relatively constant environments, slope is a physiological character of genetic meaning, is suggested from an experimental study of growth in *Platypoecilus maculatus* (Felin 1951).

For each of the year classes tested, two distinct *y*-intercepts, or levels, for transformations of mean calculated and observed lengths are maintained in the northern and southern areas. From the covariance tests, the differences are significant at the 1-percent level. Further translated into predicted ultimate size $\left(\frac{y\text{-intercept}}{1-k}=l_\infty\right)$, the range of the means for San Pedro is 220–236 millimeters standard length, and for Canada, 249–258 millimeters, with no overlap for those year classes tested (table 3).

TABLE 3.—*Growth characteristics in northern and southern areas of catch derived from regressions of means* l_{n+1} on l_n

Year classes	Rate of deceleration, slope (k)		*y*-intercept levels		Ultimate size (mm.) $\left(l_\infty=\frac{y\text{-intercept}}{1-k}\right)$	
	British Columbia	San Pedro	British Columbia	San Pedro	British Columbia	San Pedro
1937	0.57	0.54	108	102	251	222
1938	.55	.52	112	107	249	223
1939	.54	.59	115	94	250	229
1940	.52	.55	120	99	250	220
1941	.52	.56	123	101	256	230
1942	.53	.53	121	111	258	236

BIOLOGICAL SIGNIFICANCE OF DIFFERENCE IN GROWTH CHARACTERISTICS

Significant difference in level, or the growth characteristic l_∞, may represent phenotypic response of a plastic genotype to varying hydrographic environments. It may be useful as an indicator, as suggested for vertebral counts in European pilchard (Ruivo 1950) to separate homogeneous populations of certain fishing areas without implying genetic significance. The results of the covariance tests apply only to mean growth curves, and at present it seems probable that if significant difference were found in the growth characteristic *k* in certain individuals or segments of the population it would indicate genotypic difference.

There is some evidence that deviations from the straight-line regression for each area are greater for mean observed lengths of a year class in successive seasons of catch than for mean calculated lengths of a year class in one season. To compare transformations of mean observed lengths with those of mean calculated lengths is rather difficult since observed lengths are not obtained until the scales have one ring, or the fish are in their second year of life, when they have accomplished much of their growth; whereas, calculated lengths begin at 1-ring, and this first growth increment as already noted shows great variability. In San Pedro growth curves for the 1942 class, however, variance of mean observed lengths alone about the regression is 10 times the variance for calculated lengths only. Such irregularities suggest that greater shifts in populations of a given year class may occur from season to season than within one season. Small deviations from the transformations of mean calculated lengths of the 4-, 5- and 6-ring pilchard of each year class indicate that within a single fishing season the populations at each port are more homogeneous.

North-south migration of larger fish

Tagging of fish along the Pacific coast by some of the agencies engaged in pilchard research gives evidence of extensive migrations (Hart 1943a). It is the larger fish within a group tagged in the south that are caught first farthest to the north (Clark and Janssen 1945, pp. 19–20). That some of the larger pilchard cover great distances is likewise indicated in the apparent shift at older ages in central California and San Pedro toward the level of regression of northern growth types as shown in transformations of the 9-year averages of observed lengths (fig. 1).

If, however, the migration course for the entire population were of great seasonal regularity from south to north and return, one would expect with increasing age of fish a tendency toward homogeneity of growth types along the coast. If populations of older fish became more homogeneous in their growth characteristics, a given year class at 5- or 6-rings would show a tendency for the level of northern and southern growth types to shift toward a single norm of oceanic migratory sardines common to all areas of the fishery, or at least to shift toward a level and slope other than the one consistently associated with a particular area of catch. This shift does not so far occur in transformations of mean calculated length data. At 4-, 5-, and 6-rings the levels of these regressions remain distinct for northern and southern sardines (*cf.* fig. 4).

Complete intermixture and homogeneity in populations of adult pilchard in different regions of catch is not evidenced from available data on mean calculated lengths. The distinct levels of the growth transformations which are maintained in northern and southern populations, however, do not controvert the evidence from tagging that there is migration of larger fish toward the north. As is shown from tagging results, growth data also indicate migration of northern pilchard into southern waters. That larger fish of older ages enter the southern catches is demonstrated not only from the 9-year averages of observed length data (fig. 1), but likewise for a single year class as it passes through the fishery (*cf.* table 1). For San Pedro the increase in mean observed lengths for certain individual year classes at 5-ring and older is reflected in a sharp rise at this stage in their length-on-time curves of growth. Similarly, an apparent departure from an expected asymptote of length is observable in Phillips' (1948, p. 7) curve of average observed length of sardines at each age over a 6-year period at San Pedro. Such irregularity in the San Pedro growth curves must be explained by an influx onto southern fishing grounds of large, old fish differing in their growth pattern from the smaller fish up to 4-ring age which are caught in San Pedro. Conversely, in certain other year classes, there has been an actual decrease in observed lengths as a year class reached older ages and was caught off San Pedro. This indicates an influx of smaller fish of more southern growth characteristics onto these grounds. The extent of the seasonal north-south migration and the extent of season-to-season variability in interchange of northern and southern populations are as yet not determined.

Possibilities of inshore-offshore migrations of pilchard are in the main unexplored and, short of the use of radioactive markers, may be difficult to determine. Hart (1943a, p. 178), however, records tagged fish moving into inlets on the west coast of Vancouver Island and remaining there throughout the winter. Such winter fish, according to Hart, "are occasionally captured during the winter herring fishing season and . . . they sometimes provide early in-shore fishing before the main pilchard shoals approach the Vancouver Island coast in the summer."

North-south variation in growth characteristics

The variation in growth of pilchard from north to south may prove to be a physiological characteristic of clinal significance. The study of intraspecific clines in fishes is, of course, complicated by what Mayr (1944, p. 135) terms the "strong and only rather recently appreciated phenotypical plasticity of many species." It seems likely that the greater size of fish in northern waters is not entirely explained by northern migration of the larger individuals of each year group. These northern pilchard may represent a separate stock grown to larger sizes rather than only a sorting out of larger fish from a whole coastal population. It may be that such growth differences from north to south can be explained in part by geographical gradients in environmental factors associated with gradients in morphological and physiological characters, or clines, within the range of a species.

It seems probable from existing evidence on growth characteristics of the fish in different geographical regions that there may be season-to-season fluctuations in the size and the location of optimum living areas associated with fluctuations in marine climate. Such fluctuations may largely determine what part of the sardine population will be available for capture in each area. Illustrative of between-season shifts in populations are the apparently greater deviations in mean observed lengths than in mean calculated lengths of a year class from its rectilinear transformation. But it also seems evident from back calculated lengths that there is, for a given year class, a persistent cline in growth characteristics from north to south, and that populations, although fluctuating in distribution from season to season and somewhat migrant, may be more discrete and limited latitudinally than has been supposed from the evidence of vertebral counts (Clark 1936, 1947) and tagging (Hart 1943a; Clark and Janssen 1945).

McHugh (1950) has reported on latitudinal variation in three species of clupeoids of the North Pacific. Parallel gradients in hydrographic and meristic characters and consequent homogeneity or heterogeneity of populations with respect to certain characters are discussed. For the northern anchovy (*Engraulis mordax*) and Pacific sardine, McHugh found clines in anal fin-ray counts and significant heterogeneity among several populations. He notes close parallelism in meristic counts of anal fin rays in anchovy and sardines and likewise in vertebral counts of both species. From his more complete study of meristic characters in anchovy, McHugh concludes (p. 58) that "clines in numbers of dorsal, anal and pectoral fin rays are in the opposite direction to that shown for gill-rakers, and all four fail to correspond with the distribution of mean vertebral number."

McHugh considers it probable that in the Pacific Northwest the fixation period for sardine fin-ray counts occurs during a period of warmer water temperatures, while in southern California water temperatures average lower at this period of development. Thus the usual inverse relation between meristic count and temperature follows for counts of fin rays as well as of gill rakers, and to a lesser degree of vertebrae.

Lack of significant differences in vertebral counts between samples of sardines from British Columbia to southern California (Clark 1936, 1947), and the heterogeneity in populations according to fin-ray counts, McHugh attributes to close dependence of each meristic character on coexistent physical factors in the environment at the time of fixation of the character. Since spawning occurs within a rather narrow temperature range, phenotypic variation could likewise be narrow for a character, such as vertebral number, with an early fixation period, whereas with a later, perhaps longer, fixation period there could be greater concomitant variability in environmental factors and heterogeneity of populations as indicated by these other meristic characters.

McHugh's results on vertebral counts thus agree with Clark's; and he concludes (p. 110)—

> Since the number of vertebrae drops very sharply with decreasing latitude off Baja California, it is assumed that these fish belong to a distinct race that has different temperature requirements.[1] It is also concluded that the number of vertebrae is not a particularly critical measure of population segregation in pelagic spawning species.

McHugh further suggests that—

> intermingling between populations may not be random with respect to meristic or other characters. If this is so, wandering of individuals, as shown by tag returns, may not necessarily indicate movements of the population as a whole. Experimental verification of these deductions is much needed . . .

The apparent cline in growth characteristics suggests the presence of intraspecific populations in which there is limited intermingling. Rather than a general coastwise migration pattern, a series of overlapping coastal migrations of more than one stock appears more consonant with observed data on growth.

Growth characteristics determined by origin

There is increasing reason to suppose that the geographic origin of sardine populations may be widely variable from season to season. Evidence from spawning studies demonstrates that there were, during 1949 and 1950, two centers of spawning; one, early in the year, around and to the south of Cedros Island off central Lower California, and another, somewhat later and farther offshore, off southern California. It is also reported (California Cooperative Sardine Research Program 1950, p. 37) that "In the waters separating these two spawning centers very little spawning has been encountered during either season, and this little has been confined to a coastal strip . . ." During these two seasons there was little indication of northern spawning. In 1940, however, an unusual abundance of young fish of the 1939 year class was reported (Walford and Mosher 1941) in north Pacific waters off Oregon, Washington, and British Columbia. The probable occurrence of northern spawnings of lesser magnitude is suggested by the presence in other seasons of small, presumably 1-ring, pilchard in British Columbia waters recorded by Hart (1943b). The growth characteristics of northern and southern populations may thus be early determined by their origins.

Whether the populations sampled by northern and southern fisheries have genetically distinct components has not been demonstrated. The significantly different levels of their mean growth transformations may indicate only phenotypic differences in growth ascribable to differing environmental conditions at time and place of spawning or in later life or both. These differing conditions of growth must largely be maintained, however, in each area and in each population sampled, since the mean levels of growth transformations characteristic of each geographic region have remained relatively constant and distinct as shown from calculated length data for 4-, 5-, and 6-ring sardines of each of six year-classes over the seasons of study. This appears to point to the conclusion that there may be a southern spawning center which contributes more heavily to the southern California stocks and that although some of the more southern growth types migrate into central California, they are found rarely in the Pacific Northwest.

The existence of an area of intense spawning off central Lower California was not realized until the expanded sardine research program under the California Marine Research Committee made possible the collection of eggs and larvae in this spawning center as well as in the better known area of more widespread spawning off southern California. In both areas, times of spawning vary between seasons and appear to be associated with conditions of favorable temperature and upwelling. (See California Cooperative Sardine Research Program 1950, p. 39.) The varying importance of the contributions of the two areas to the present sardine fisheries is suggested in differing prevalence of southern or of northern growth types in the catches. It appears to be a reasonable hypothesis that the spawning grounds off central Lower California give rise to the southern components found in the catches off San Pedro (and to a lesser degree in catches off central California), while the large northern fish originate off southern California and to the north in years favorable for northern spawning. It is not yet known whether spawning populations in the two main centers are or are not distinct, i. e., genetically isolated in space and time.

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[1] From data obtained in the California Cooperative Sardine Research Program in 1949 and 1950, the spawning requirements, so far as temperature is concerned, have been closely similar in what at present appear to be the two main centers of spawning (1) off central Lower California and (2) southern California.

Fish in the northern part of the range of the fishery are perhaps distinguishable as large, long-ranging individuals, while southern stocks may be characterized by smaller size and more limited migration routes. These stocks appear to overlap in their distribution on fishing grounds as evidenced from the length-frequency data accumulated over a long period of years by the California Department of Fish and Game and later by the State agency in cooperation with the United States Fish and Wildlife Service. Over the period of study of age composition of the catch for which length composition by age is also available, it is evident that the smaller sizes of each year class are rarely caught north of central California.

Ronquillo (1949, p. 29) found that the sizes of pilchard in the Pacific Northwest during most months of fishing did not differ significantly from those caught off central California, but that fish from both these regions showed significant differences from those taken off San Pedro. Over three seasons, from 1945–46 through 1947–48, in all age groups there was a significant difference in size between fish landed at San Pedro and Monterey. During the first 2 years of life sardines taken at San Pedro were significantly larger; in older age groups those landed at Monterey were larger than those at San Pedro. Ronquillo (op. cit., p. 25) also found that the coefficient of variation fluctuated more at San Pedro than at other localities which indicated greater heterogeneity in those samples. He found this measure relatively constant in the Pacific Northwest and therefore indicative of homogeneity within the samples.

The tendency for smaller sizes to remain in the southern part of the range of the species is illustrated also by tagging results (Clark and Janssen 1945, p. 22). They found a southward migration of some of the sardines released in central California and note—

> a greater proportion of the smaller sizes have made this southward migration. For the group tagged in 1940, 72 percent of the recoveries in southern California during the first season after tagging were less than 19 cm. when tagged. For the same season in central California only 50 percent of the recoveries were of these smaller sizes. During the second season after tagging, 74 percent of the southern California recoveries were less than 19 cm. when tagged but only 43 percent of the central California recoveries were composed of these smaller sizes.

Recoveries of sardines tagged off central Lower California have been almost entirely in California. Approximately 78 percent were recovered in southern California, 15 percent in Monterey, 7 percent in San Francisco and less than half of 1 percent (represented by one tag) in Washington (Janssen 1948). Concerning the absence of recoveries in Lower California, Janssen (p. 7) states as follows:

> No tag recoveries have been reported from reduction plants in Lower California. Facilities for recovering tags were in operation there for only a brief period and the quantity of sardines processed in Mexico is small in comparison with other localities along the coast.

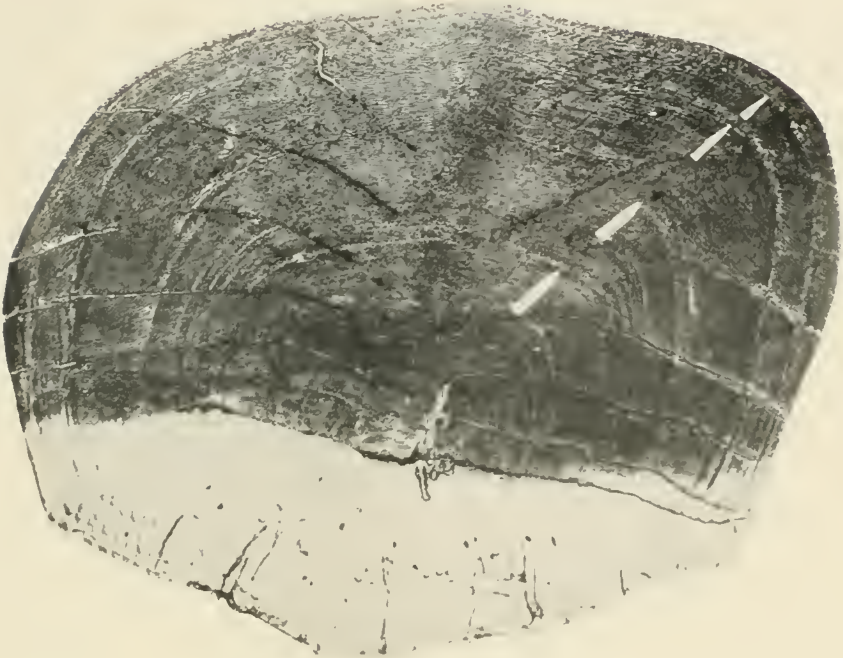
Considering the total number of tags recovered without regard to area of recovery, only 10 percent of tags put out off Mexico were recovered, while off southern California 23 percent and off central California 25 percent were recovered (according to Janssen's adjusted percentage recovery figures, p. 9). The Mexican taggings further indicate the tendency for the southern fish to remain in southern waters.

The larger pilchard of a year class, on the other hand, commonly are caught on any of the usual fishing grounds from the Pacific Northwest to southern California. Whether the significant difference in attained ultimate size, l_∞, of southern as opposed to northern growth types arises by reason of primary difference either in location of spawning centers or in location of nursery grounds, or both, and whether in turn difference in origin of stocks also represents genetic difference await further data from spawning studies and determination of how discrete are the areas of spawning and of spawning stocks.

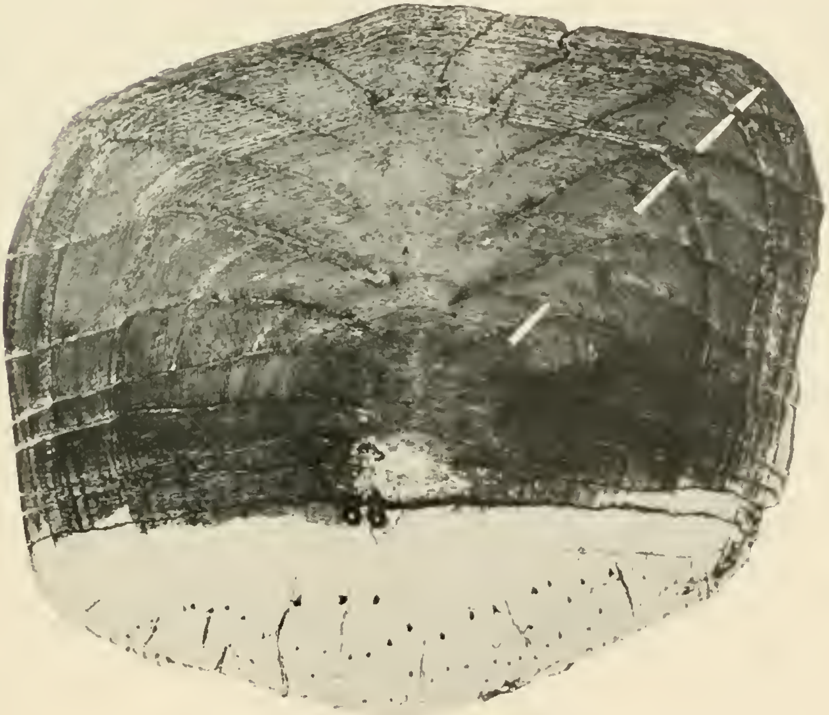
The apparent differences in growth characteristics in populations along the coast suggest the desirability of study of population dynamics not only for the coast as a whole but also for geographic areas, e. g., for the Pacific Northwest, central California, southern California, and further subdivisions of areas off Lower California not yet clearly delineated.

SCALE AND GROWTH PATTERNS OF INDIVIDUAL FISH

That the fished stocks of the Pacific Northwest and southern California have, for practical purposes, some independence seems indicated from further lines of evidence.

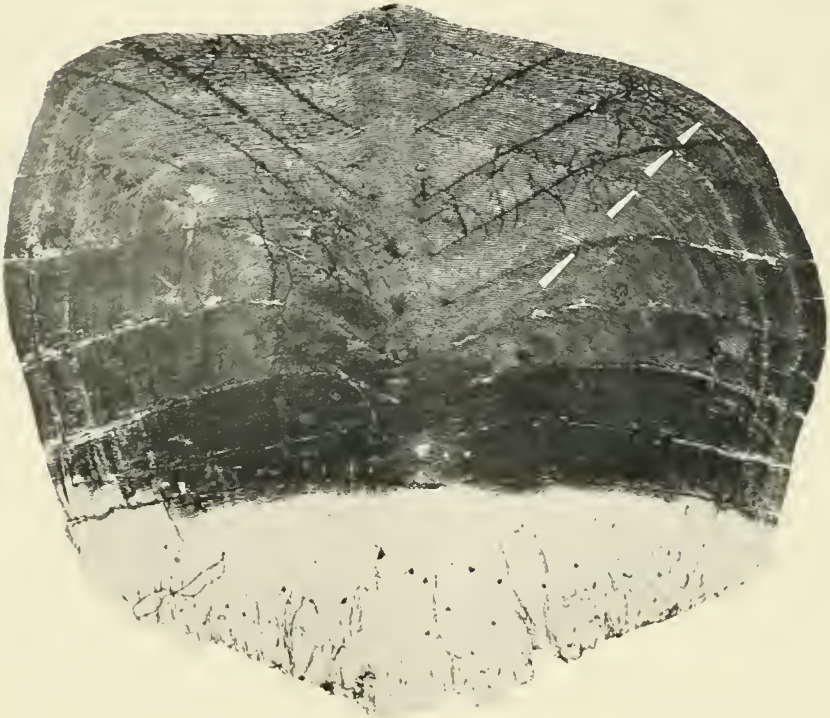


(1) Northern type from Canada (219-mm. female)

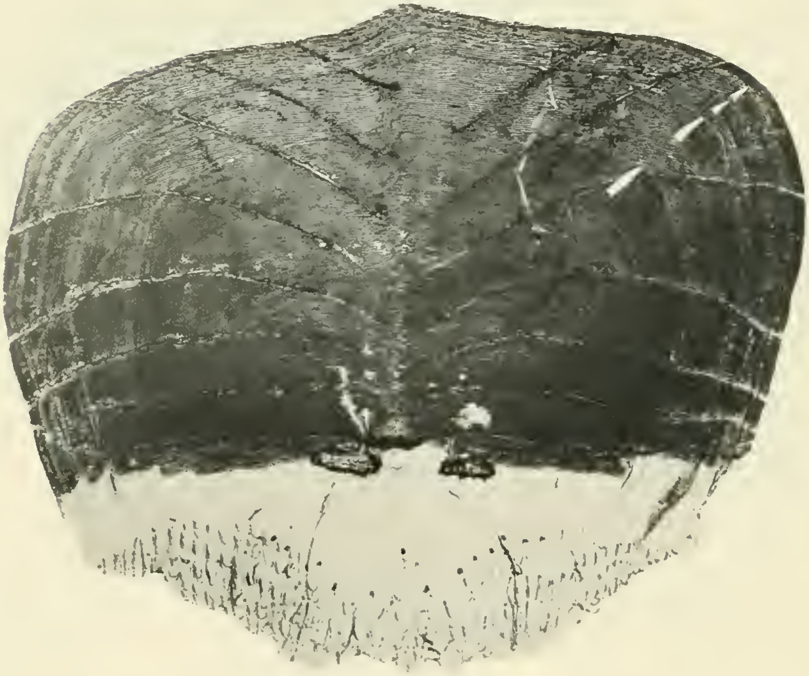


(2) Northern type from San Pedro (211-mm. female)

FIGURE 5a.—Growth types of Pacific pilchard at 4-ring stage as shown in scale patterns. These scales show the well-defined annual rings of large fish caught commonly in the north, but also entering the southern fishery. They have a proportionately small first-growth increment and a rapid rate of deceleration in growth.



(3) Southern type from San Pedro (206-mm. male)



(4) Southern type from San Pedro (204-mm. female)

FIGURE 5b.—Growth types of Pacific pilchard at 4-ring stage as shown in scale patterns. These scales show fainter year marks common among smaller fish in southern catches, rarely caught in the north. The proportionately large first-growth increment is common to both; (3) shows slow deceleration, (4) fast deceleration.

Early in the examination of scales for age determination, qualitative differences were noticed in the scale patterns of pilchard from different regions of catch. An attempt was made to establish criteria for separating ring types somewhat as had been done in herring by Norwegian investigators (Runnstrøm 1936). Although scales collected in the Pacific Northwest showed predominantly heavily marked winter rings of the northern type associated with sharp cessation of growth (*cf.* fig. 5a), and those from the San Pedro fishery showed, as a rule, the faintly marked annuli suggesting milder winters (*cf.* fig. 5b), the presence of intermediate ring types in central California made the separation too subjective for quantitative treatment.

Further attempts to separate the varying growth patterns in individual fish were made using transformation values (calculated by the method of semiaverages) asymptotic length (l_∞) and rate of deceleration of growth (k) for individuals caught in four geographical regions. For the 1939 class, the regression of the values l_∞ on k gave scatter diagrams (fig. 6) for Canada (N=286, dots) and San Pedro (N=433, circles). Even though there is overlapping in the scatter of individuals caught in the two areas, a large proportion of 4-ring sardines of the growth type caught in San Pedro are outside the scatter for the Pacific Northwest. This type was characterized by relatively steep slope, or slow rate of deceleration, and small calculated ultimate size. We interpreted this to mean that there was in turn a large proportion of San Pedro 4-ring fish that would never have been caught in the Pacific Northwest. Likewise, a smaller proportion of Canadian fish were outside the San Pedro scatter and might never be caught in southern California.

Scatter diagrams (fig. 7) of San Francisco (N=514, symbolized by x) and Monterey (N=783, symbol Q) show many fish of the northern type. Numerous individuals from Monterey catches also fall within the scatter of characteristically San Pedro type (*cf.* fig. 6). San Francisco shows few of the latter but a large proportion of types common to Canada; namely, with relatively rapid deceleration rates and greater asymptotic lengths.

These regressions of l_∞ on k for 1939-year-class pilchard caught in the 1943–44 season were curvilinear as in the aquarium fish *Platypoecilus maculatus*, and some individuals with improbably high calculated asymptotes [2] were found as in platies (Felin 1951).

Similar regressions for individual pilchard of the same year class were plotted at the 6-ring stage (fig. 8). By this time, individuals of an unlikely predicted ultimate size were not represented in the catches anywhere along the Pacific coast and calculated asymptotes were well within the probable range of size for the species. As a result of the disappearance of these types, the regressions appear linear.

The scatter for 6-ring pilchard at all four ports included 194 individuals. Of these, 10 percent were entirely outside the main scatter of all fish. This group showed southern growth characteristics. Out of 70 from Canada only 1 percent were of this type with slow deceleration rate and low predicted size. Of 54 fish from San Francisco, 11 percent were of this type; of 57 in Monterey, 7 percent; and out of the small number, 13, of this older age caught at San Pedro, 62 percent had the typically southern growth characteristics.

The high percentage of these fish in San Pedro is in agreement with the appearance of predominantly southern-type annuli in San Pedro scales. Many scale samples taken from sardines off southern California and a few collected off Lower California show faint winter marks and wide zones of summer growth; the yearly increments decrease very slowly in size, illustrative of their slow deceleration in growth. (See figure 5b.) These fish are characteristically of small size for their age compared with northern types (see fig. 5a), and so far have not been observed to attain as great age as the large northern pilchard. Their position in this respect appears similar to that of the warm-water Mediterranean pilchard when compared with North Sea types (*cf.* fig. 2).

From the few available samples of Mexican fish taken off northern Lower California there is also indication of another southern growth type characterized by a low k value (the slope is even less than that for northern types), and by a small calculated ultimate size. (See figure 5b.)

The pilchard scales were photographed by means of infrared plates. This method was used by Roper (1936), to bring out year rings as distinct

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[2] J. L. Hart (personal communication) recorded a standard length of 351 mm. for a pilchard caught off the west coast of Vancouver Island and landed at Nootka.

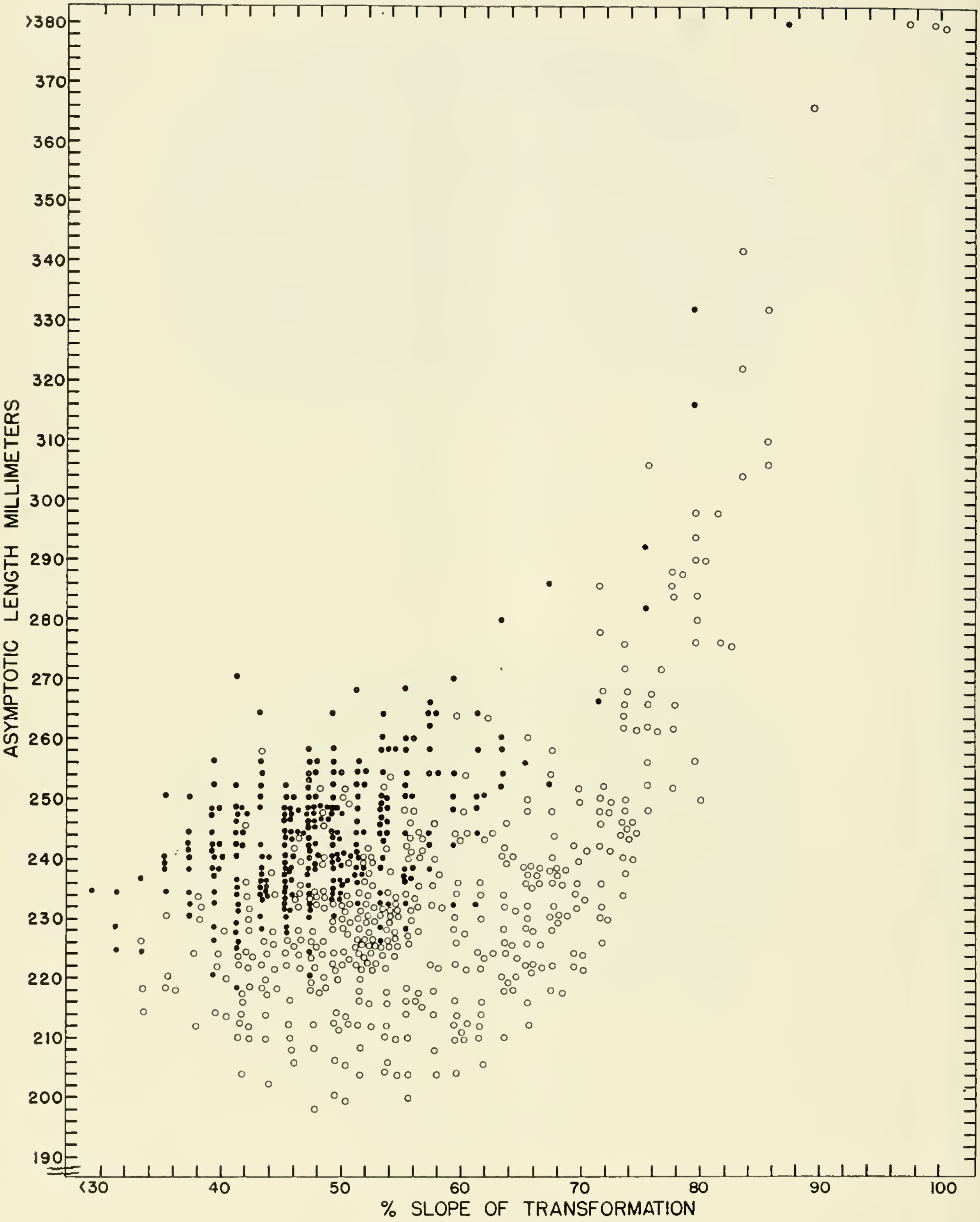

FIGURE 6. Regression of transformation values calculated for individual pilchard of 1939 class caught at the 4-ring stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Dots represent fish taken in Canada, circles in San Pedro.

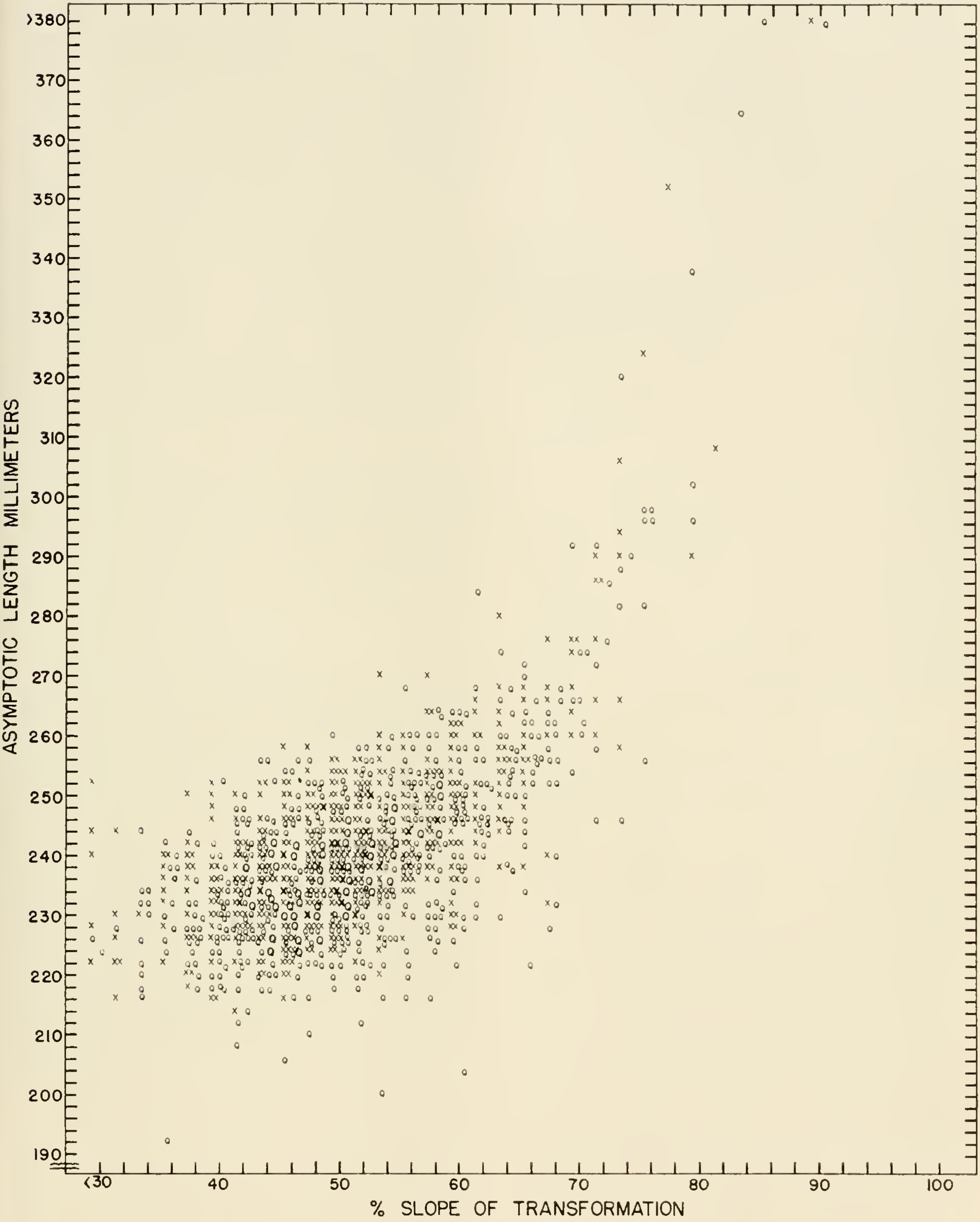

FIGURE 7.—Regression of transformation values calculated for individual pilchard of 1939 class caught at the 4-ring stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Symbol x represents fish taken in San Francisco, symbol Q in Monterey. Larger symbols represent values for five fish, smaller for a single individual.

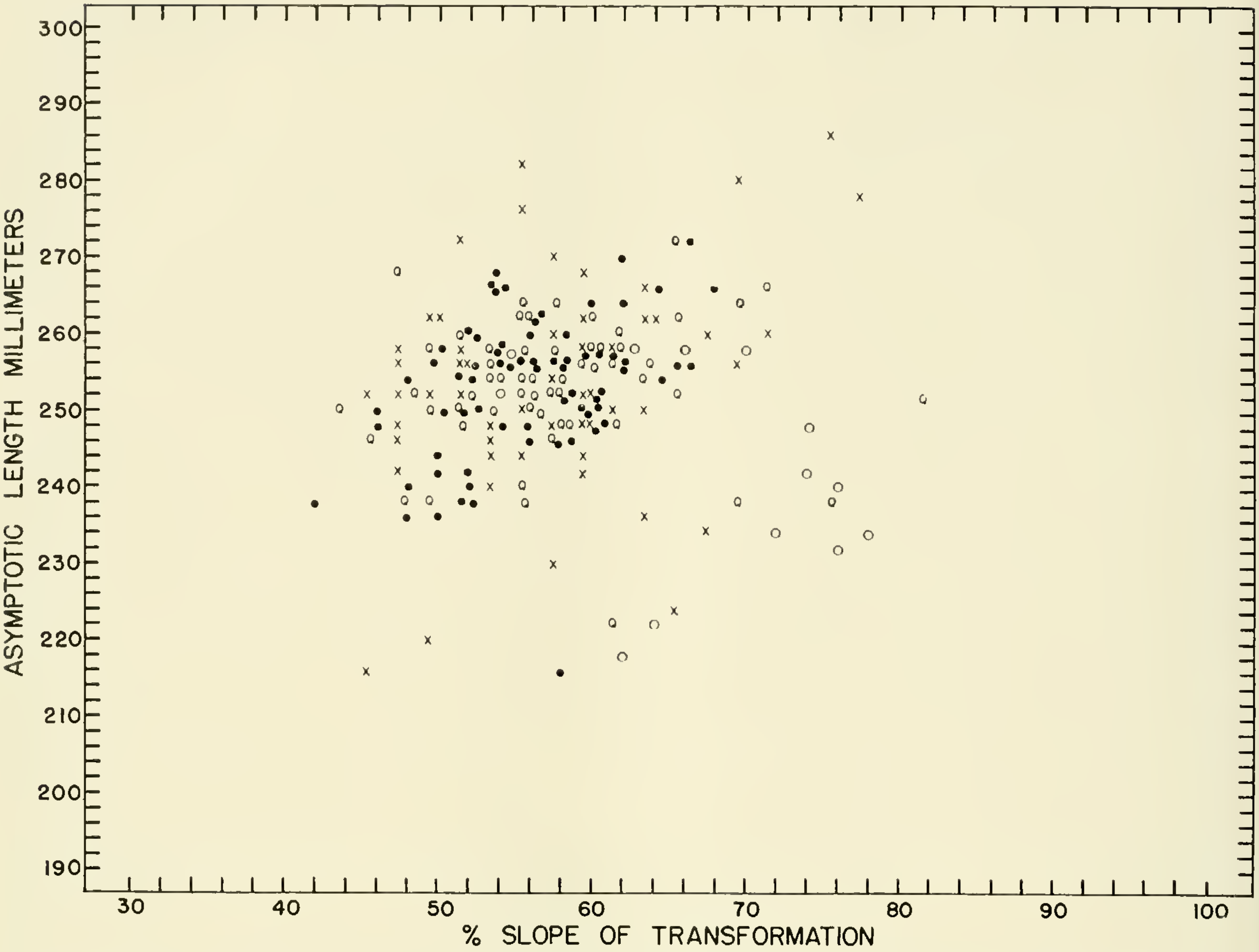

Figure 8.—Regression of transformation values calculated for individual pilchard of 1939-class caught at the 6-ring stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Dots represent individuals taken in Canada, circles San Pedro, symbol x San Francisco, symbol Q Monterey.

from false rings in opercula of perch, and appears a satisfactory means of photographing pilchard scales.

Hessle (1925) gives illustrations of scale types which show differing growth patterns in various races of Baltic herring. The autumn-spawning herring which spawn in coastal waters (never inside archipelagoes) show rapid growth during the first 3 years and subsequent rapid falling off in growth increments. This is likewise the growth pattern of the somewhat smaller, spring-spawning sea herring of the Baltic in the same region. (The pattern corresponds to pilchard growth with a low k value, or rapid rate of deceleration in growth.) The fjord herring, on the other hand, also spring spawners, are sometimes quite isolated and show great variability in size with some dwarf and some giant forms. Hessle notes (p. 37) that "these two herring forms [dwarf and giant] show a striking similarity as regards actual mode of growth." He figures (p. 40) the "even growth" typical of all the fjord herrings as contrasted with the "stagnant growth" (pp. 17, 33) of sea herring of the Baltic. He also found (p. 45) ice herring in the Gulf of Bothnia with a growth pattern and spawning habits similar to the fjord herring. He concludes that—

> mode and rate of growth seems . . . to be very like that of the most rapid-growing fjord-herrings of the Middle Baltic. It is therefore natural to suppose that these spring-spawners of the Gulf . . . are closely related to the fjord-herring of the Middle Baltic.

The even-growth pattern of Hessle corresponds to the southern growth type of the Pacific sardine with a high *k* value, or slow deceleration in growth.

CONTRACTION OF FISHED STOCKS

Recent catch data may be pertinent also to the problem of populations. The abrupt decline in landings of pilchard in recent seasons reached a low of 130,000 tons in 1947–48, the lowest in the history of the fishery on the Pacific coast since 1923–24 (Anonymous 1948). To account for this decline, a number of explanations have been offered by pilchard investigators, all of which may affect in varying degrees the fished population(s): (1) Lowered recruitment of young fish, (2) reduced availability of fish to the fisherman, (3) increased natural mortality, and (4) increased fishing mortality.

The decline in catches in central California and in the Pacific Northwest have been almost entirely responsible for the sudden decline in total catch of the coast as a whole. In all these ports there has been poor fishing since the 1945–46 season and in the Northwest there were no landings during the 1949 and 1950 seasons.

In southern California, however, the total catch did not fall off conspicuously up to 1950–51, and in this season San Pedro recorded the largest tonnage of sardines ever taken there. The catch per unit-of-effort did fall in 1947–48 (Clark and Daugherty 1950, 1952), but for no other recent season has it differed greatly from previous average lunar months. Concentration of sardines on southern grounds has been used as argument by representatives of the industry to obtain legal extension of Monterey grounds 70 miles to the south (Monterey Herald, May 14, 1951).

Contraction of areas of good fishing and apparent contraction of spawning areas may be dependent on hydrographic changes, and centering of the available population in the southern part of the range thus may have produced a series of southern year classes.

DISTINGUISHING SOUTHERN AND NORTHERN YEAR CLASSES

To detect early in its life in the fishery a year class that is likely to be primarily southern, some measure of its relative strength in northern and southern areas of catch is desirable. One measure of strength of a year class in the fishery has been the numbers of pilchard in the 3-ring stage caught at all ports (Walford 1946b). Although availability and degree of recruitment at earlier ages are more variable, another measure of early strength of a year class in any region is the number of 1-ring or 2-ring fish caught at any port. At this age presumably, migrating pelagic sardines would be less widely dispersed throughout their possible habitat and nearer their point of origin.

San Pedro is considered the port nearest centers of spawning. Early strength of a year class at this port may be taken as a measure of spawning success in the south. Figure 9 shows ratios of catch per boat-month (using California catch-per-unit data, Clark and Daugherty 1950) at San Pedro to catch per boat-month [3] for the coast as a whole for 1-ring (dot) and 2-ring (circle) sardines of each year class over the period of comparable sampling (1941–49). The year-class strength for the Pacific coast as measured by catch per boat-month at the 3-ring stage is also figured (symbol x). (There is rather close correspondence between year-class strength at 2-ring and at 3-ring. For the 1947 year class, the number caught at 2-ring is figured, by symbol +, as an approximation of its probable strength in the following season.)

When the ratio of San Pedro 2-ring fish to the Pacific-coast total was low, as in the 1939 year class, the total year-class strength for the whole coast was well above average. The 1940 year class was slightly above average strength; the ratio San Pedro to Pacific coast was somewhat above 1.0 at 1-ring, somewhat greater at 2-ring. The 2-ring age group usually dominates at San Pedro. The 1941 class, however, was the dominant age group as 3-ring at San Pedro in 1944–45, showed a high ratio to the rest of the coast, was somewhat below average in year-class strength, and was relatively below normal numbers in northern ports throughout its life in the fishery. By these criteria, the 1939 year class may be called a successful year class with early strength in the northern fishery, the 1941 class relatively

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[3] When estimates of total numbers of sardines caught, by year class, are used instead of those adjusted for fishing effort the results correspond closely.

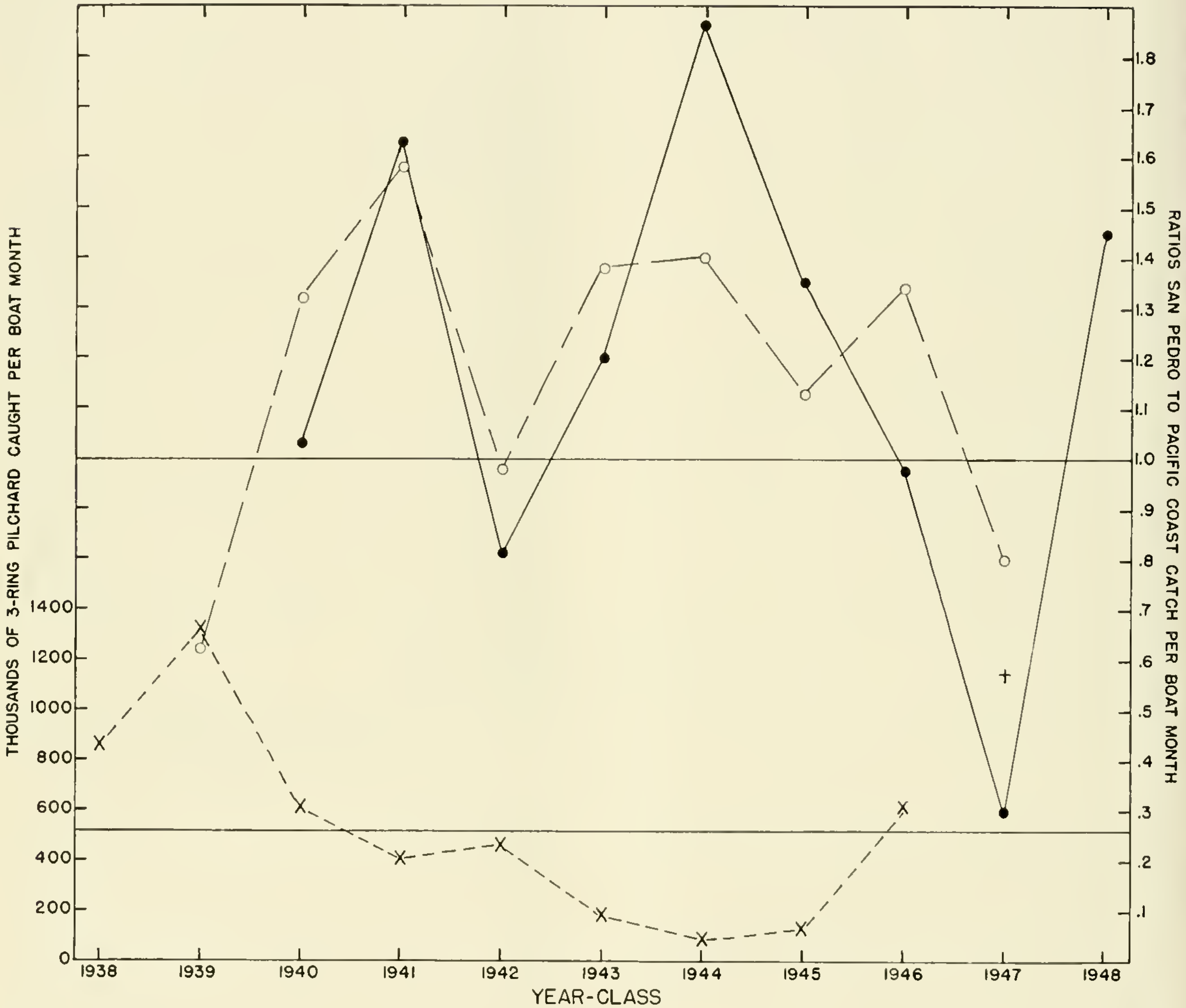

FIGURE 9.—Ratios of numbers of pilchard of each year class taken per unit-of-effort at San Pedro to those taken along the whole Pacific coast as 1-ring (dot), as 2-ring (circle). Numbers of fish of each year class taken per unit-of-effort at the 3-ring stage are shown (symbol x) as relative measures of year-class strength.

less successful and primarily a southern year class.[4] The 1942 class was of about average strength and the San Pedro-Pacific coast ratio indicated probable northern origin. The year classes 1943, 1944, and 1945 were below average strength and showed early dominance at San Pedro as compared with the rest of the coast. The 1946 year class was above average strength and the San Pedro-Pacific coast ratio was below 1.0 at 1-ring, although comparatively in greater numbers as 2-ring at San Pedro. The 1947 class appears the most successful of any year class since that of 1939, and it shows a low San Pedro-Pacific coast ratio.

From these data the existence of southern and northern year classes seems indicated. Early northern strength, or a low ratio, may prove indicative of a widespread spawning and a relatively successful year class. There also are indications that a strong southern year class, such as those of 1941, 1946, and probably 1948, can make such significant contributions to southern catches that their year-class strength when measured by numbers caught along the whole coast at 3-ring still can be considerable. It is nevertheless only those year classes 1943, 1944, and 1945 which appear predominantly southern, by these criteria, that so far have been much below normal strength.

The San Pedro to Pacific coast ratios at 1-ring may be a better measure of relative year-class strength by region than ratios at 2-ring. There are apparent wide variations in availability, as well as in recruitment, of pilchard at 1-ring as shown in total numbers of this age class caught during each season at each port (*cf.* Felin and Phillips 1948: Mosher et al. 1949; Felin et al. 1949; Felin et al. 1950; Felin et al. 1951). Such wide variations are likely to be associated with the origins of each year class. By the time sardines have reached 2-ring they may be more widely dispersed and their origins more obscure. Hart (1943a, p. 174), for example, noted that two fish, probably of the 1939 year class, tagged at Monterey by the California Bureau of Marine Fisheries, were taken off the Canadian coast early in 1941, presumably at the 2-ring stage.

In general, the assumption that 1- and 2-ring fish have not traveled great distances is substantiated by the behavior of tagged sardines of these approximate sizes. Data from Janssen (1938) and Clark and Janssen (1945) show that recoveries to the north of fish from the southern California tagging area are at first of larger sizes than commonly would occur in the 1- and 2-ring age classes. It is also evident from Phillips' (1948, p. 7) average length-on-time growth curves for the Pacific Northwest, central California, and southern California, that for the 6-season period (somewhat subsequent to the tagging data) the mean observed lengths at 1- and 2-ring are greater for San Pedro fish than for those caught in the Pacific Northwest. In central California, 1-ring fish average smaller than those in the other two areas. At 2-ring, central California sardines begin to exceed the sizes at San Pedro. At 3-ring the sizes of Pacific Northwest pilchard begin to exceed those caught in the other two areas. These data indicate that few large 1- and 2-ring fish have left the southern California area.

Further evidence that the larger 1-ring and 2-ring sardines have not migrated far from the southern grounds is provided by calculated length data (table 4). At 1-ring the mean calculated first growth increment, $\bar{l}_1$, is greater at San Pedro than at Monterey for all the year classes over the 9-year period of study. At 2-ring, for nearly all year classes the $\bar{l}_1$ still is greater in the southern area. By the time the year classes have reached 3-ring the situation has reversed and the calculated first growth increments are nearly all greater in central California, indicating a strong influx of southern fish with large $\bar{l}_1$ into the area. For nearly all year classes at 4- and 5-rings of age the average calculated first growth increment continues to be greater at Monterey than at San Pedro.

Ronquillo (1949, p. 12) found statistically significant difference in mean observed lengths of 0- and 1-ring fish in San Pedro and Monterey and concluded that "fish reared in these two areas do not intermingle at this age." Since the commercial fishery is carried on in the winter off California when growth is minimal and the first ring will soon

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[4] William T. Miller (ms.) found that temperature conditions in the spring of 1941 were unusually warm in the area off Lower California during February and March, and that according to United States Hydrographic Office records, water temperatures were higher than those normally associated with pilchard spawning. His charts suggest that during this season temperatures favorable for spawning were restricted both in space and time, namely to the area off southern California. He contrasted the 1941 season with the 1939, an unusually cold spring, and showed that during the latter season temperatures off Lower California were favorable for spawning over a wide area in February, March, and April. Water temperatures suitable for the widespread northern spawning known to have taken place in 1939 were also recorded. The relative scarcity of fish of the 1941 year class in northern catches might thus be attributed to contraction of areas and time of spawning.

TABLE 4.—*Calculated mean first growth increments* ($\bar{l}_1$) *for pilchard year classes from 1- to 5-ring caught at San Pedro and Monterey, 1936–48*

Year class	1-ring				2-ring				3-ring				4-ring				5-ring			
	San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey	
	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$
1936																	47	104	42	104
1937													160	105	193	107	53	102	159	108
1938									1,169	98	1,054	100	453	96	672	101	100	98	351	102
1939					1,707	93	2,512	94	1,293	92	1,581	95	424	96	1,146	97	174	98	534	103
1940	256	121	313	118	1,287	109	554	107	807	106	934	110	413	103	470	108	44	105	71	107
1941	332	115	69	98	1,069	103	253	100	1,134	98	350	103	151	100	153	101	26	107	43	111
1942	386	108	563	96	1,042	98	1,376	96	242	102	319	103	60	116	81	109	46	109		
1943	523	105	446	104	335	101	254	107	189	107	140	115	83	115			10	116		
1944	106	114	74	107	259	128	96	110	161	126			33	133			27	130	30	131
1945	370	143	327	117	281	139	100	99	99	131	23	114	60	133	62	132				
1946	195	109	357	107	407	112	59	103	209	117	172	116								
1947	59	123	613	104	242	121	503	101												
1948	71	140	14	133																

appear, the observed length at 0-ring is comparable to the calculated length at 1-ring, and observed length of 1-ring fish is comparable to the calculated length at 2-ring.

Tagging and growth data thus both appear to indicate a tendency for larger fish to migrate farther north, but there is apparently not a great deal of emigration of the large 1- and 2-ring sardines from the southern California grounds so that these early ages may be used as reasonably good indices of early year-class strength in one geographical area.

ANOMALIES IN YEAR-CLASS CATCH CURVES

Vital statistics of the fishery show that new sources of fish were unexpectedly available in season 1949–50 (Felin, Daugherty, and Pinkas, 1950 and 1951). The overavailability of certain ages is reflected in certain anomalies in year-class catch curves at all California ports. At all three ports there was a marked deviation from the previous trend of total mortality rate for 1944 and 1945 year classes, as 4- and 5-ring fish. In central California ports, the 1943 and 1946 year classes also showed increase in availability (as defined by Marr 1951).

BIMODALITY IN LENGTH-FREQUENCY COMPOSITION

There are also indications of bimodality in length-frequency composition of the 1944 year class caught during the 1949–50 season in California ports (Felin, Daugherty, and Pinkas, 1950).

Study of growth transformations from calculated lengths of individual fish of the 1944 year class showed that coincident with the unexpectedly large catches of this year class as 5-ring fish in 1949–50 there were many small-sized individuals of this age caught in San Pedro and Monterey. Some of these 5-ring fish were smaller than sardines of the same year class as 4-ring so that their presence in the catches could not be accounted for as small fish remaining after the exodus of larger migrants going north. Their presence must rather be explained as an influx, probably from the south, of small fish into the southern and central California fishing areas. That this appears to be a strongly southern year class is indicated in figure 9. The average observed lengths of the 1944 year class as 5-ring at San Pedro and Monterey also show a decrease as compared with the same year class caught as 4-ring fish in the previous season.

An appearance of bimodality has also been observed in the length composition of other year classes in previous seasons (*cf.* Felin and Phillips 1948), and is further evidence from growth that pilchard caught along the Pacific coast do not constitute a single homogeneous population.

SUMMARY AND CONCLUSIONS

1. The question whether the fished stocks of the Pacific pilchard, or sardine, along the Pacific coast are homogeneous is considered in the light of evidence from growth studies and other vital statistics.

2. The direct proportionality of growth of scale to growth of fish is used to obtain approximations of mean calculated lengths of sardines.

3. Walford's (1946a) transformation plot is applied to mean observed length data and mean calculated length data sampled in different regions.

4. Comparison is made of growth characteristics, k (slope of the regression, or rate of deceleration of growth) and l_∞ $\left(\frac{y\text{—intercept}}{1-k}\text{, or calculated ultimate size}\right)$ of six year classes sampled in the most northern region of catch, Canada, and the most southern, San Pedro.

5. From analysis of covariance no significant differences are evidenced in the mean slopes, k, of the transformations between each of these six year-classes in Canada and San Pedro.

6. For each year class tested, two distinct y-intercepts, or levels, of mean transformations are maintained in the northern and southern areas, and from the covariance tests the differences are significant at the 1-percent level. The growth characteristic l_∞ thus differs significantly in the northern and southern catches.

7. The use of the straight-line transformation as a method of expressing growth differences not readily apparent in conventional length-on-time growth curves was noted by Walford (1946a). The applicability of the usual statistical tests of significance to such regressions of l_{n+1} on l_n is now also apparent. Possible meanings of significant difference in k and l_∞ as physiological characters are discussed.

8. Complete intermixture and homogeneity in populations of adult fish as sampled by the fishery in different regions is not evidenced from data on mean calculated lengths.

9. The apparent cline in the growth characteristic l_∞ appears indicative of intraspecific populations in which there is limited intermingling, and suggests a series of overlapping coastal migrations of more than one stock.

10. The recent discovery of an area of intense spawning off central Lower California, more or less discrete from the widespread spawning area off southern California, points to the tentative hypothesis that spawning grounds off Lower California give rise to the southern components found in catches off San Pedro (and to a lesser degree off central California), while the larger fish originate off southern California and occasionally to the north.

11. Evidence from qualitative and quantitative differences in individual scale and growth patterns indicates some independence in the fished stock of the Pacific Northwest and southern California.

12. The decline in catches in central California and the Pacific Northwest has been almost entirely responsible for the sudden decline in total catch of the entire coast. It is suggested that the centering of the available population in the southern part of the range may have produced a series of southern year classes.

13. Ratios between year-class strength of 1- or possibly 2-ring fish taken at San Pedro and taken along the coast as a whole may prove a useful index in determining whether a year class is primarily southern or has more northern components.

14. The measure of year-class strength used by Walford (1946b), i. e., the number of 3-ring pilchard caught at all ports, is compared with the San Pedro–Pacific coast ratios of 1- and 2-ring fish. To date only those year classes which appear predominantly southern by these criteria have been much below normal strength.

15. Vital statistics of the fishery which indicated that new sources of fish became unexpectedly available in the 1949–50 season appear to be explained at least in part by an influx, probably from the south, of small fish onto the southern and central California fishing grounds.

16. Bimodality in length-frequency composition is further evidence from growth that pilchard caught along the Pacific coast do not constitute a homogeneous population.

17. Whether heterogeneity in growth characteristics is the expression of genotypic difference or a phenotypic response of a species to its environment is not yet determined.

18. In view of differences in stocks on the various fishing grounds along the Pacific coast, the study of population dynamics not only for the coast as a whole but also by geographic areas appears desirable.

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BIOTIC INFLUENCES AFFECTING POPULATION GROWTH OF PLANKTONIC ALGAE

By Theodore R. Rice

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BIOTIC INFLUENCES AFFECTING POPULATION GROWTH OF PLANKTONIC ALGAE

By **THEODORE R. RICE**, ***Fishery Research Biologist***

The enormous fluctuation in abundance of phytoplankton in oceans, lakes, and ponds has attracted the attention of oceanographers and limnologists for over half a century. Many hypotheses have been advanced to explain this phenomenon. The common belief has been that the abundance of each species, the size of the total population, and the succession of species during the season are controlled by changes in the physical factors or by a lack of the necessary nutrients, or by a combination of the two influences. Attention has also been called to the action of filter-feeding animals in reducing the numbers of the phytoplankton.

The further suggestion has been made that the intensive growth, or bloom,[1] of one species might affect the growth of another species, thus exerting an influence on the seasonal succession of species in the body of water concerned. Akehurst (1931) made a study of phytoplankton in fresh-water ponds over a period of 4 years. All attempts to correlate fluctuations with chemical and physical factors failed. Therefore, he reasoned that other factors such as the complicated action of toxins were very important. These toxins were believed to originate from the phytoplankton and were defined as "excretion products which serve as accessory nutrients," inhibiting the growth of some species of phytoplankton and stimulating the growth of others. He further believed that the toxins of a particular species not only inhibited its own further growth after a certain length of time, but that the toxins of the "oil producing group" of algae inhibited the growth of some species and stimulated the growth of other species in this group while all members of the "starch group" were stimulated. The same general action of toxins of the "starch producing group" were also suggested. While Akehurst made very detailed studies in the field, it is believed by the author that his conclusions which treated all algae as either oil or starch producers are too general. A study of this complicated type of interaction should be made between species and preferably under controlled laboratory conditions.

More recently it has been shown in laboratory cultures of planktonic algae that metabolites, or other biological influences, of a species tend to inhibit the growth of that species. Pratt and Fong (1940) grew cultures of *Chlorella vulgaris* in inorganic medium for different periods of time and until different population sizes had been obtained. The cells were then removed by filtering the culture medium. This filtered culture medium, which shall be referred to as "conditioned medium," was used in different proportions with fresh medium after the pH had been adjusted to prepare new cultures of *Chlorella*. The growth of *Chlorella* in this medium was found to be slower than in culture medium to which no "conditioned medium" had been added. The conclusions Pratt drew from these experiments are as follows: (1) That the growth of *Chlorella* is inhibited by the presence of the "conditioned medium" in the culture medium; (2) that the depression of growth increases as the percentage of "conditioned medium" increases; and (3) that for a given concentration of "conditioned medium" in the culture medium, the depression of growth varies inversely with the size of *Chlorella* population in the "conditioned medium" prior to filtering.

NOTE.—This paper is a revision of a thesis that was submitted to Harvard University in 1949 in partial fulfillment of the requirements for the degree of doctor of philosophy. The author acknowledges his sincere appreciation to Dr. George L. Clarke, for stimulating criticism and kindly encouragement which contributed much to the completion of this work.

[1] The terms "bloom," "flowering," "outburst," and "pulse" refer to a rapid increase in the numbers of phytoplankton above the level of abundance previously existing in the area. No numerical value has been agreed upon which defines a bloom, but population densities above 1 million cells per liter have been commonly referred to as blooms. A bloom is often accompanied by a coloring of the water.

An apparent case of algal antagonism, similar to that observed by Pratt, was reported by J. Storey (Worthington 1943), who found that the water of Lake Windermere, when an *Asterionella* bloom is disappearing, is unsuitable for the preparation of culture medium for *Asterionella*. This suggests the possibility that *Asterionella* produces a substance similar to chlorellin produced by *Chlorella*. Experiments also showed that *Skeletonema* produces a substance which inhibits its further growth (Levring 1945).

Rodhe (1948) has conducted experiments on the effects of growing two species of planktonic algae in a common medium. He found that *Asterionella formosa* cultured in the presence of *Chlorella* had a lower rate of division than when grown alone, but a detailed study of the interaction was not made. Since completion of the present investigation the author has learned of the work of Lefevre, Nisbet, and Jakob (1949). These investigators reported inhibition in the growth of some species of algae by "algastatic" substances secreted into the medium by other species of algae. They tested the growth of several species of algae in culture medium prepared with filtered medium in which *Scenedesmus* had previously grown and in other culture medium prepared with medium in which *Pandorina* had previously grown. Most of those species tested in these media grew at a slower rate and later the cells of some shrank and died.

The purpose of the present study was to ascertain whether the biological products of a species could influence its own growth as well as the growth of another species under conditions which could be tested in laboratory cultures, and to consider whether these materials actually do exert an effect under natural conditions.

PREPARATION OF CULTURES

Two species of fresh-water algae, *Chlorella vulgaris*, class Chlorophyceae, and *Nitzschia frustulum*, class Bacillarieae, were used in these experiments. The author is grateful to Dr. W. T. Edmondson for a subculture of *Chlorella* and to Dr. Ruth Patrick for identifying the *Nitzschia*. Also the author appreciates the assistance of Dr. E. G. Pringsheim in isolating the *Nitzschia* into pure culture. *Nitzschia frustulum* was originally isolated by the author from a mixture of algae obtained from the Carolina Biological Supply Company. This is the first record that this species of *Nitzschia* has been isolated and cultured in the laboratory.

LIQUID CULTURE MEDIUM

These experiments required that both *Nitzschia* and *Chlorella* grow well in the same culture medium, thus increasing the difficulty of finding a suitable medium. Many of the better-known culture media were tried but were found to be unsatisfactory for the growth of one or the other of these algae. The author, therefore, devised a nutrient culture medium which proved to be satisfactory for the growth of both *Nitzschia* and *Chlorella*.

Only Pyrex glassware was used and it was cleaned with a mixture of sulfuric acid and potassium dichromate, followed by a thorough rinsing first in tap water and then in distilled water. The culture medium was always autoclaved at least 1 day prior to the time it was to be used, since many investigators have stated that the growth of algae is inhibited if autoclaved medium is used sooner. The formula for this medium which will be referred to as standard culture medium is as follows:

$Ca(NO_3)4H_2O$	0.04 gram
$MgSO_4 \cdot 7H_2O$	.02 gram
KCl	.04 gram
Na_2SiO_3	.025 gram
$FeCl_3$	.001 gram
KH_2PO_4	10 μgAP
"A-Z" solution	1 cubic centimeter
Double-distilled H_2O	1,000 cubic centimeters

An "A-Z" minor nutrient solution, containing small quantities of a number of elements thought to be necessary for plants, has been suggested by Hoagland and Snyder (1933). This solution, modified by omitting the $CuSO_4 \cdot 5H_2O$ and TiO_2, was added to the standard culture medium.

STERILITY

These experiments were conducted on bacteria-free cultures, as tested from time to time by streaks made on nutrient agar containing 2 percent glucose and ½ percent peptone. *Chlorella* was maintained in a pure state by culturing it on agar slants prepared with Detmer's (diluted to two-thirds its normal strength) and Bristol's solutions, both containing 2 percent glucose and ½ percent peptone. Only Detmer's solution was used for culturing *Nitzschia*.

ILLUMINATION OF CULTURES

A set of four 40-watt daylight fluorescent bulbs was arranged on each of the four shelves in the culture cabinet. Approximately 5 inches above each set of lights was a platform made of glass which had been ground with carborundum to ensure an even dispersal of light and on which were placed the cultures of algae. In these experiments, daylight fluorescent lamps were used which produced an illumination on the culture flasks of 375-foot candles as measured by a Weston illumination meter. The cultures were illuminated daily from 11 a. m. to 1 a. m.

TEMPERATURE

The culture cabinet was placed in a dark constant-temperature room. In these investigations a temperature of 18°±1.5° C. was maintained. The temperature variation was checked with a maximum and minimum thermometer. Two circulators were used to blow a stream of air over the cultures, thus ensuring an even distribution of temperature.

INORGANIC-PHOSPHATE DETERMINATION

Phosphate concentrations were determined by the Atkins-Denigès molybdate method as modified by Wattenberg (1937). Algal cells were removed by filtering the culture medium through a sintered glass filter before making determinations. The concentration of phosphorus is expressed as microgram-atoms of phosphate phosphorus per liter as recommended by the International Association of Physical Oceanography (Sverdrup et al. 1942; table 42).

PREPARATION OF ALGAL CELLS FOR EXPERIMENTS

Ketchum (1939) and Pratt (1940) both found that the growth of algae when transferred to fresh medium was influenced by the age of the culture from which the cells were taken. Cells from older cultures had a longer lag period and a slower rate of growth. Therefore, in these experiments *Chlorella* cells were always taken from a 6- to 7-day-old culture, while *Nitzschia* cells were taken from a 4- to 5-day-old culture.

The cells were removed from the culture medium in which they were growing by centrifuging at 2,500 r. p. m. for approximately 5 minutes. The cells were resuspended in the same type of culture medium which was being used in the experiment. A cell count was made on this concentrated suspension of cells so that the proper dilutions could be made to give the desired concentration of cells for the experiment.

DETERMINATION OF POPULATION SIZE

After thoroughly mixing the culture medium, 0.5 cc. was removed aseptically. This medium was used for making two cell counts with a Levy haemocytometer. The mean of the numbers of cells counted in all like cultures in any one experiment was taken as the population size. A careful check showed that this method is extremely accurate for determining unialgal population sizes. At the lowest population sizes used in these experiments, this counting method showed a coefficient of variation of 7.1 percent, while the largest population sizes gave even more accurate results, with a coefficient of variation of 4.6 percent. The accuracy of this method as determined by the author agrees favorably with that found by other investigators (Pearsall and Loose 1937; Pratt 1940; and Winokur 1948).

GROWTH RATES AND INTERACTIONS OF *CHLORELLA* AND *NITZSCHIA*

GROWTH CURVE AND DIVISION RATE OF *CHLORELLA*

Since it has been observed that phosphorus occasionally reaches concentrations as high as 10 μgAP/L in natural waters (Chandler and Weeks 1945), the growth rate of *Chlorella* was determined in culture medium containing this concentration. Standard culture medium was prepared with *Chlorella* in a concentration of 70 million cells per liter and placed on the illuminated shelves. At the end of each day cell counts, the pH (as determined with a Beckman pH meter), and phosphorus determinations were made for one culture.

The *Chlorella* population (fig. 1) was still increasing on the seventh day even though all the measurable phosphorus had been used by the end of the fourth day. Ketchum (1939) had shown that *Chlorella pyrenoidosa* when grown in a nonnutrient medium divides until the phosphorus

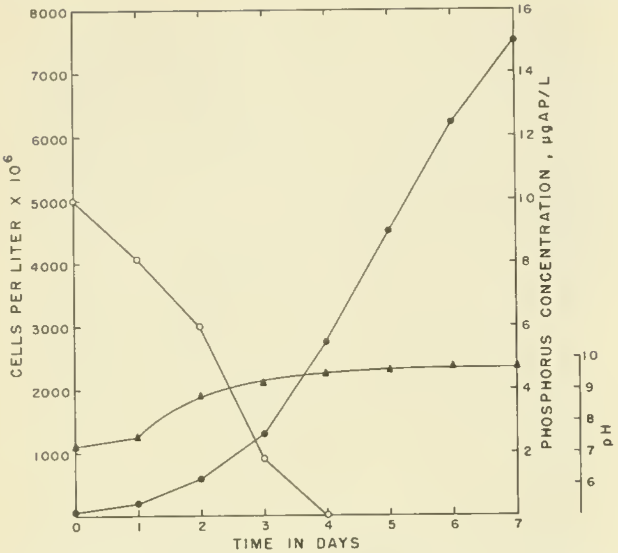

FIGURE 1.—Growth curve of *Chlorella* in standard culture medium. Dots represent growth curve of *Chlorella*; circles, phosphorus concentration; triangles, pH.

in the cells is reduced to one-half the normal content. Thus the cells in this experiment probably were able to continue dividing after all phosphorus disappeared from the medium by using intracellular phosphorus absorbed in excess of that needed during the first 4 days of the experiment. The division rate for *Chlorella* (fig. 2) was greater on the second than on the first day. The division rate on the third and fourth days was about the same as on the first day. From the fourth day through the seventh there was a steady decrease in the division rate.

Determinations of pH made at the end of each illumination period, when the culture medium was found to be most alkaline, are shown in figure 1. The pH rose from 7.2 on the first day to 8.3 on the second day, and continued to increase daily during the illumination period for the duration of the experiment. Determinations made at the end of each period of darkness showed that the pH had dropped each day to about 7.0 or 7.2.

GROWTH CURVE AND DIVISION RATE OF *NITZSCHIA*

The growth curve of *Nitzschia* under similar conditions of adequate nutrients was obtained by following the procedure described for *Chlorella* except that cultures were prepared with 10 million *Nitzschia* cells per liter. As shown in figure 3, the *Nitzschia* population reached a peak on the fifth day and was relatively constant for the remainder of the experiment. The division rate as shown in figure 4 varied from 1.5 to 1.2 on the first 3 days of the experiment and decreased rapidly on the fourth and fifth days. All measurable phosphate in the culture medium had been used by the end of the fifth day. Very little division occurred on the sixth day, and there was none on the seventh day. It appears that *Nitzschia* cells cannot continue to divide for as long a time as *Chlorella* cells after phosphorus has disappeared from the medium. It was found that *Chlorella* cells divide for 3 days after phosphorus disappears from the medium while *Nitzschia* cells divide for only 1 day. This may be due to *Chlorella* cells when grown in the presence of phosphorus absorbing much more than needed while *Nitzschia* cells grown in the presence of phosphorus may absorb only that needed for immediate use. The pH concentration, measured at the end of the light period, increased from day to day and reached a peak at the end of the third day. Beginning on the fifth day and continuing through the seventh day, the pH did not increase as much at the end of the light period as on previous days. Since the culture medium was not buffered, the pH increased as the size of the population increased. Thus the smaller increase in pH from the fifth day on was probably due to a reduced metabolic rate.

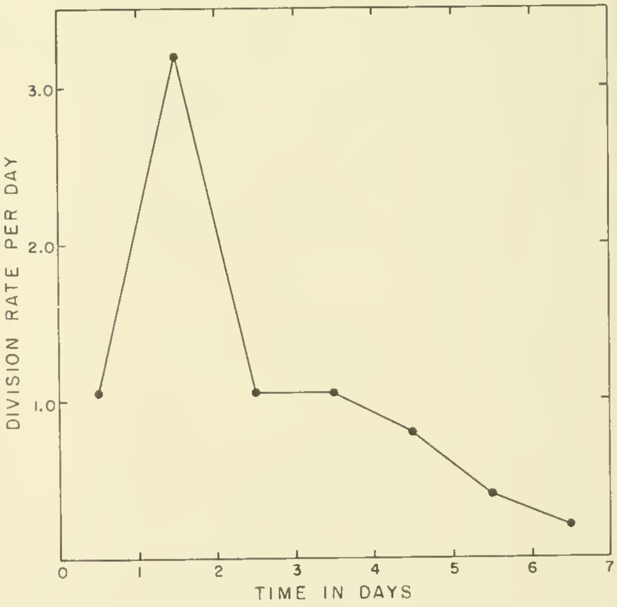

FIGURE 2.—Division rate of *Chlorella* in standard culture medium.

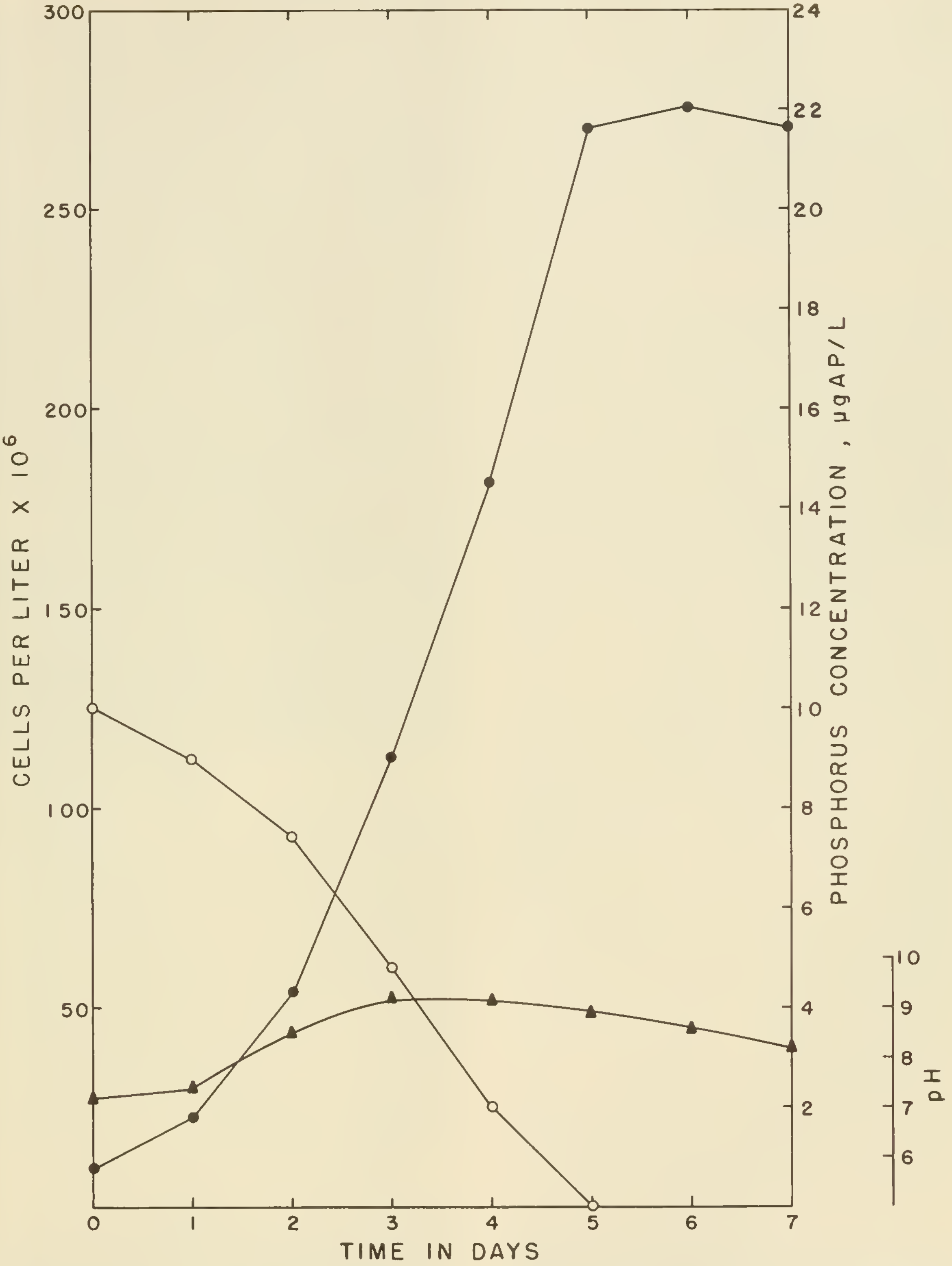

FIGURE 3.—Growth curve of *Nitzschia* in standard culture medium. Dots represent growth curve of *Nitzschia;* circles, phosphorus concentration; triangles, pH.

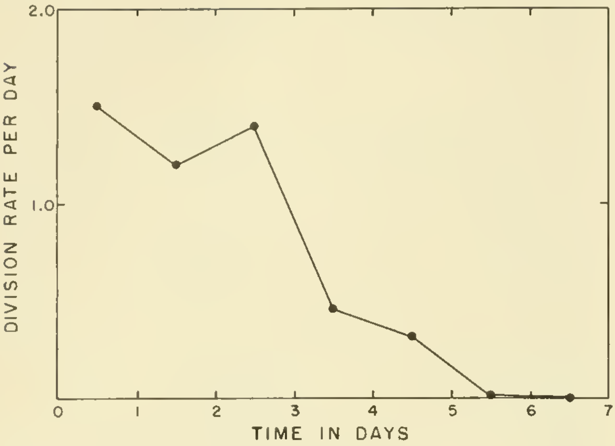

FIGURE 4.—Division rate of *Nitzschia* in standard culture medium.

INTERACTIONS OF *CHLORELLA* AND *NITZSCHIA*

To test whether or not one species of phytoplankton may inhibit the growth of another, the following experiment was run in which *Chlorella* and *Nitzschia* were grown together in mixed culture. The same procedure was followed in this experiment as described in the foregoing experiments, except that both *Chlorella* and *Nitzschia* were added initially to each flask.

Chlorella grown in mixed culture under the conditions of this experiment reached a population size only 60 percent of that attained when grown alone in the same type of medium (fig. 5); also the division rate was significantly less than when grown alone (fig. 6). There was considerable difference in the division rates on the second day and *Chlorella* grown in mixed culture continued to divide at a slower rate for the remainder of the experiment. *Nitzschia* in mixed culture reached a population size which was not significantly different from that obtained in the cultures in which *Nitzschia* was grown alone (fig. 7), and the division rates of *Nitzschia* under these conditions varied only slightly.

Even after taking into consideration the error of counting and the ordinary fluctuation occurring between two different cultures, it is evident that the results for *Chlorella* are significant. It was also found later that *Chlorella* can inhibit the growth of *Nitzschia* under certain conditions. Other investigators have shown that several algae inhibit their own growth, while in this experiment it has been demonstrated that a species of alga can also inhibit the growth of another species. Pratt and Fong (1940) reported that *Chlorella* produces and liberates into the culture medium an antibiotic substance which they named chlorellin. This author believes that *Nitzschia* also produces an antibiotic substance which inhibited the growth of *Chlorella* in the experiment described here. Further experiments supporting this conclusion are presented later.

Referring again to figure 5, it is seen that the phosphorus was depleted by the end of the fourth day in the mixed culture. However, this also occurred in the *Chlorella* culture (fig. 1). The pH increased a little more rapidly and was slightly higher in the mixed culture than in either the *Chlorella* or the *Nitzschia* cultures. Therefore the possibility must now be considered that the observed inhibition of *Chlorella* was due to either a depletion of nutrients or an unfavorable change in pH concentration instead of the production of an antibiotic substance by *Nitzschia.*

In initially enriched medium:

To determine whether a lack of nutrients had limited the growth of either or both *Chlorella* and *Nitzschia*, experiments similar to the preceding ones were run again with twice the initial concentration of nutrients in the culture medium. In the cultures in which *Chlorella* and *Nitzschia* were grown alone and in mixed cultures, the sizes of

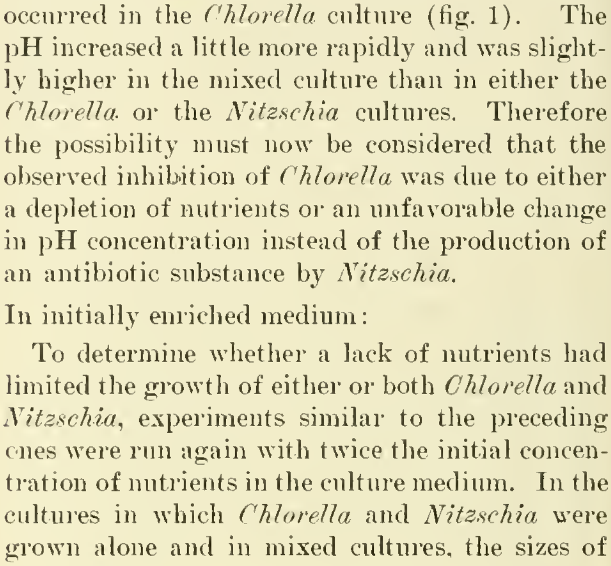

FIGURE 5.—Comparison of growth curves of *Chlorella* in *Chlorella* culture and in mixed culture prepared with standard culture medium. Dots represent growth curve in *Chlorella* culture; circles, growth curve in mixed culture; X's, phosphorus concentration; triangles, pH.

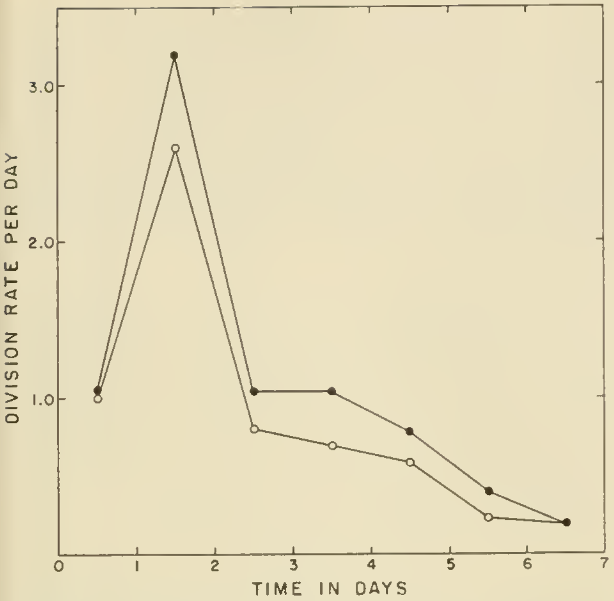

FIGURE 6.—Comparison of division rates of *Chlorella* in *Chlorella* culture and in mixed culture prepared with standard culture medium. Dots represent division rate in *Chlorella* culture; circles, division rate in mixed culture.

the populations reached on the seventh day in this experiment with twice the amount of nutrients was not significantly different from those obtained in the previous experiments. Also the division rates did not vary significantly.

In medium enriched daily:

Since nutrients may inhibit the growth of some algae if present in too high a concentration, the preceding experiment was repeated except that the extra amount of nutrients was added daily from the end of the second day through the sixth day. This method made possible tests on the effect of higher concentrations of nutrients without increasing the initial concentration. To the first group of flasks, an amount equal to 10 percent of the initial concentration of nutrients was added to each flask. To the second group an amount equal to 30 percent, and to the third group an amount equal to 50 percent of the initial concentrations of nutrients was added daily to each flask.

At the end of these experiments, the size of the populations reached in the *Chlorella*, the *Nitzschia*, and the mixed cultures were not significantly different from those obtained in the two previous experiments. Division rates obtained for *Chlorella* when grown in the presence of *Nitzschia* in mixed cultures were lower than division rates of *Chlorella* grown alone. As was found in previous experiments, division rates for *Nitzschia* were as high when grown in the presence of *Chlorella* as when grown alone. From the results of this and the previous experiment, it can be concluded that a lack of nutrients is not responsible for the observed inhibition of growth rate of *Chlorella*.

In buffered medium:

In the first experiment testing interactions between *Chlorella* and *Nitzschia* the hydrogen-ion concentration increased considerably, especially as the cultures aged. To test whether the growth of either *Chlorella* or *Nitzschia* had been limited by this change, experiments were run in which the hydrogen-ion concentration was prevented from fluctuating as widely. In this experiment the culture medium was buffered at pH 7.2 with .001 molar KH_2PO_4 and K_2HPO_4. The same

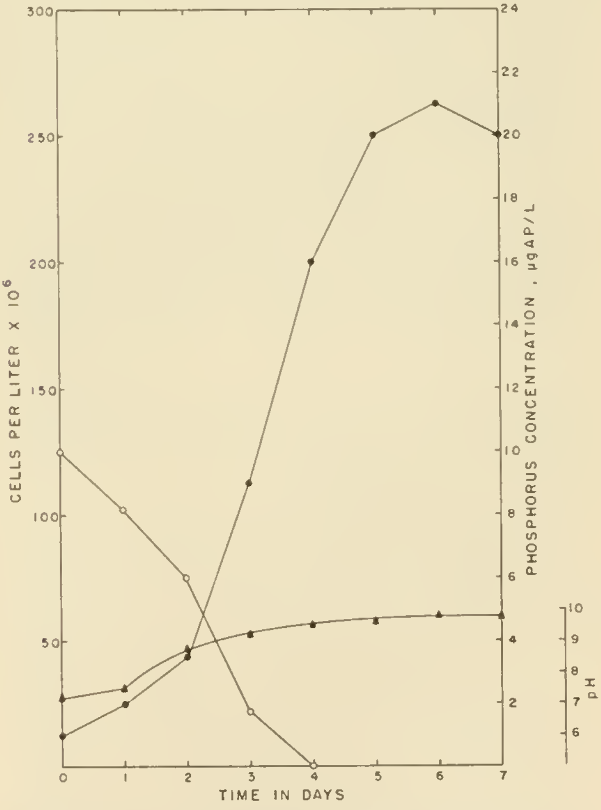

FIGURE 7.—Growth curve of *Nitzschia* in mixed culture prepared with standard culture medium. Dots represent growth curve of *Nitzschia*; circles, phosphorus concentration; triangles, pH.

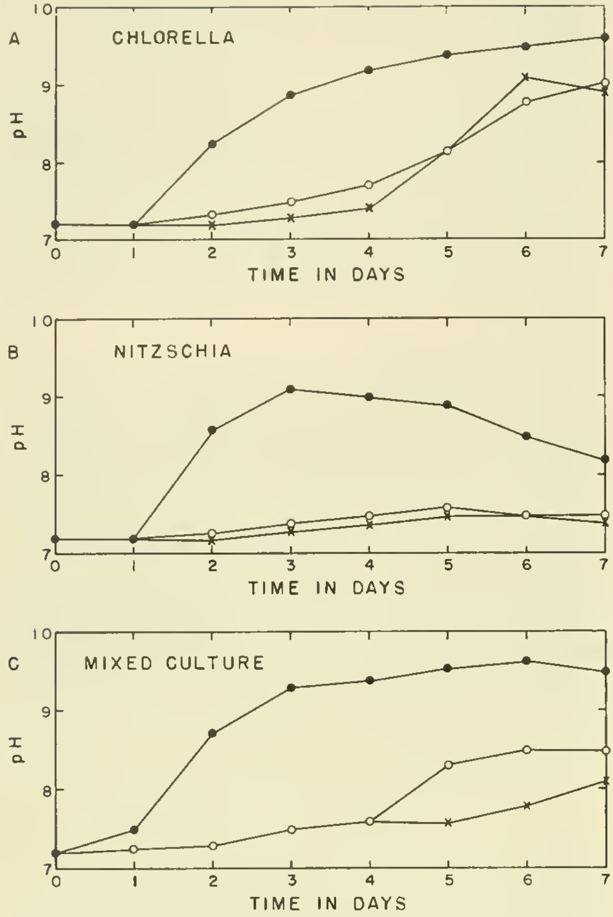

FIGURE 8.—Comparison of pH changes in unbuffered, buffered, and aerated culture media. Dots represent pH changes in unbuffered culture medium; circles, pH changes in medium buffered with .001 molar KH_2PO_4 and K_2HPO_4; X's, pH changes in aerated medium.

procedure used in previous experiments for the preparation of cultures was followed. At the end of each day for 7 days, cell counts and a pH determination were made.

The greatest pH concentration reached in any of the buffered and aerated cultures during the first 4 days of the experiment was 7.7 (fig. 8, A, B, and C) and it was not exceeded during the fifth, sixth, and seventh days in the *Nitzschia* culture (fig. 8, B). In the buffered flasks a pH of 9 was reached on the seventh day in the *Chlorella* culture, while in the mixed cultures the pH increased to only 8.5 on the sixth and seventh days. *Chlorella* cells growing alone had a higher rate of growth than the *Chlorella* cells in mixed culture. When compared with the results of the previous experiments, there was no significant difference in the total population sizes or the division rates for either *Chlorella* or *Nitzschia* when grown alone, and a similar inhibition of *Chlorella* occurred in the mixed cultures as in the previous experiments. Therefore pH can be eliminated as the factor responsible for the observed inhibition of growth of *Chlorella* in the mixed cultures.

In aerated medium:

Another experiment was run in which the pH was prevented from fluctuating as widely as in unbuffered medium by bubbling air through the culture medium during the period of illumination. In addition to preventing as great a fluctuation in pH, this method also furnished a larger supply of carbon dioxide for photosynthesis.

In this experiment, seven flasks were each fitted with a rolled cotton-wool plug through which an air inlet tube extended to the bottom of the flask so that air could be bubbled through the culture medium. A cotton filter, consisting of a calcium chloride drying tube filled with cotton-wool, was attached to the air inlet tube of each flask and the entire apparatus was autoclaved. *Chlorella* cultures were prepared in each flask with a concentration of 70 million cells per liter. The air from an air pump was run into a jar fitted with a rubber stopper containing seven outlet tubes arranged in a circle around the inlet tube. This apparatus was placed on the illuminated shelves and one flask of *Chlorella* was attached to each outlet tube. At the end of each day for 7 days one culture was removed. A flask containing 100 cc. of distilled water was used to replace the culture in order that the remaining cultures would continue to receive a constant supply of air. Cell counts and a pH determination were made each day for the culture removed from the apparatus. This experiment was repeated using *Nitzschia* cultures with an initial concentration of 10 million cells per liter. The experiment was run a third time using a mixed culture of *Chlorella* and *Nitzschia* in the same respective initial concentrations as before.

Chlorella grown alone under the conditions of this experiment reached a population size approximately twice that obtained in previous experiments. While the *Chlorella* population showed a

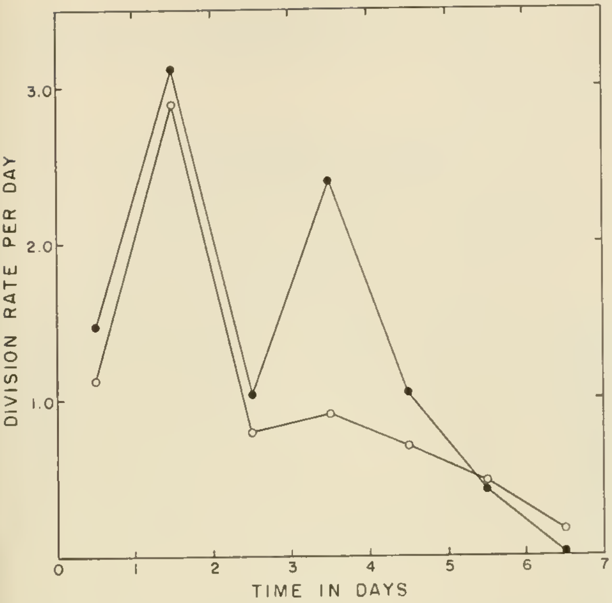

FIGURE 9.—Comparison of division rates of *Chlorella* grown in *Chlorella* culture and in mixed culture in aerated medium. Dots represent division rate in *Chlorella* culture; circles, division rate in mixed culture.

marked increase in size when grown in aerated mixed culture over that obtained when it was grown without aeration, it still reached only about one-half the population size of aerated cultures of *Chlorella* grown alone. The division rates in aerated cultures of *Nitzschia* were also larger than in unaerated cultures. The division rate of *Chlorella* when grown alone was greater than when grown in the mixed culture on every day except the sixth and seventh days when the division rates were about the same (fig. 9). It now appears beyond doubt that this inhibition of growth of *Chlorella* in mixed cultures was due not to a change in pH but to the presence of *Nitzschia*.

Nitzschia reached a total population size significantly larger when grown alone than when grown in the presence of *Chlorella*. The division rates for *Nitzschia* grown alone were generally higher than in mixed cultures (fig. 10), although the difference was perhaps not significant except on the fourth day. The relatively great depression of the division rate for *Nitzschia* in mixed culture on the fourth day may have been due to the large increase of *Chlorella* which occurred on the same day (fig. 9). The pH in the *Nitzschia* culture fluctuated only from 7.2 to 7.5 (fig. 8, B), and the growth of *Nitzschia* was significantly improved by aeration.

On solid agar:

Since solid medium has been used extensively for testing the antagonistic action of one organism on the growth of another, this experiment was designed to test the effect of chlorellin on *Nitzschia* when grown on agar. After much experimenting, it was found that *Chlorella* and *Nitzschia* grew well on agar medium prepared with Detmer's solution, diluted to two-thirds its normal concentration and containing 1 percent agar, 2 percent glucose, and ½ percent peptone. Since *Chlorella* is much less motile than *Nitzschia* when grown on agar, it was transferred to fresh agar slants which were then placed in a horizontal position 63 centimeters below a 50-watt Mazda lamp in a constant-temperature room.

After *Chlorella* had grown on the agar for 10 days, a small piece from an agar slant on which *Nitzschia* was growing was transferred to the agar slant on which *Chlorella* had been growing, being placed midway between the clump of *Chlorella* and the opposite end of the agar slant (fig. 11). It is a well-known fact that, compared with other organisms, algae grow very slowly on agar. Also algae require light to grow and the heat from the light shortens the length of time an agar slant can be used by speeding up dehydration of the agar.

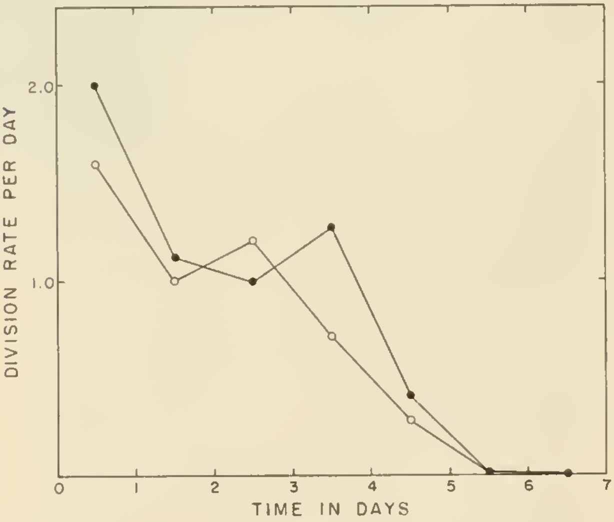

FIGURE 10.—Comparison of division rates of *Nitzschia* grown in *Nitzschia* culture and in mixed culture in aerated medium. Dots represent division rate in *Nitzschia* culture; circles, division rate in mixed culture.

This dehydration process can be partly overcome by keeping the agar slants in a cold room. However, to make this experiment feasible, it was necessary to accelerate the growth of *Nitzschia*. At this time it was discovered that by transferring a small piece of agar on which *Nitzschia* was growing (as described above) as much growth could be obtained in 1 week as was previously obtained in 4 to 6 weeks with transfers made by the conventional bacteriological streaking method.

In 3 to 5 days after *Nitzschia* was transferred to the agar slants containing *Chlorella*, it had grown as close to *Chlorella* as it would. It was quite evident that *Nitzschia* would not extend its growth so as to make contact with *Chlorella*. A small area remained between *Chlorella* and *Nitzschia* as shown at C in figure 11.

Another agar-slant experiment was run in which *Chlorella* was placed at the opposite end of the agar slant. Results were similar to those just discussed. *Nitzschia* grew most rapidly in the central portion of the slant. This was the area on which *Nitzschia* first reached a point beyond which it would grow no closer to *Chlorella*. Later *Nitzschia* covered the area to both sides of this point, leaving the same relative distance between it and *Chlorella*.

It might be thought that lack of nutrients prevented *Nitzschia* from growing until it came in contact with *Chlorella*; however, Detmer's medium diluted with distilled water to two-thirds its normal concentration still contains more of each nutrient than the liquid standard culture medium, and 16 times the total concentration of nutrients in that medium. It thus seems improbable that lack of nutrients could be responsible. Another possible cause was the use of test tubes instead of Petri dishes. The surface of the agar was not horizontal in the test tube, and this might have prevented *Nitzschia* from growing until contact was made with *Chlorella*. However, since *Nitzschia* is motile, and since it grows as rapidly upgrade as down, this factor can be disregarded. Further, as the agar was uniform in composition throughout, the sudden cessation of growth in the rapidly growing *Nitzschia* when it reached the proximity of *Chlorella* must have been due to some change in the agar so that *Nitzschia* would not grow on it. The failure of *Nitzschia* to grow on this area is believed to be due to the presence of chlorellin, the antibiotic substance shown by Pratt (1940) and in this report to be produced by *Chlorella*.

INHIBITION OF GROWTH RATE IN CONDITIONED MEDIA

INHIBITORY EFFECT ON *CHLORELLA* OF *NITZSCHIA*-CONDITIONED MEDIUM

It was found that the medium in *Nitzschia* cultures became conditioned by an accumulation of an antagonistic substance as the culture aged, so that greater inhibition in the growth rate of *Chlorella* occurred when that species was added to aged cultures than when it was added initially with *Nitzschia* to new medium. *Nitzschia* cultures with a concentration of 10 million cells per liter were prepared in six flasks with medium containing twice the concentration of nutrients used in the standard culture medium. At the end of the second day three cultures were removed from the illuminated shelves, and *Chlorella* was added in sufficient quantity to give a concentration of 70 million cells per liter; three cultures were left as controls. Also three *Chlorella* controls containing 70 million cells per liter were prepared with fresh culture medium.

Chlorella added to the *Nitzschia* cultures reached a population size about 45 percent of that obtained in the control cultures (fig. 12) and 65

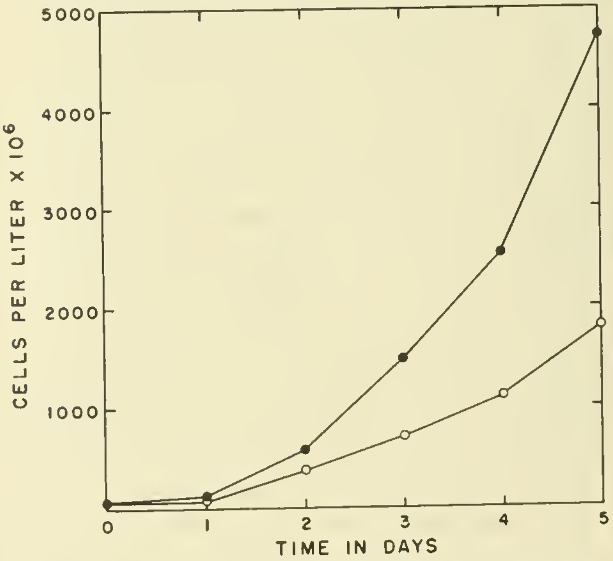

Figure 12.—Comparison of growth curves of *Chlorella* in control and in *Nitzschia*-conditioned medium. Dots represent growth curve in control cultures; circles, growth curve in *Nitzschia*-conditioned medium.

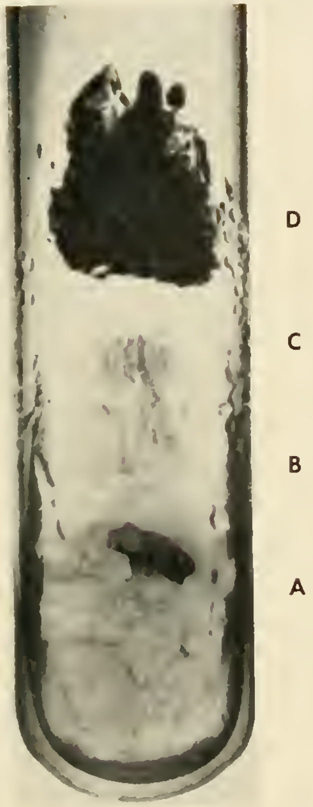

FIGURE 11.—The use of agar to demonstrate the inhibitory effect of *Chlorella* on *Nitzschia*. A. Original inoculation of *Nitzschia*. B. Area over which *Nitzschia* extended its growth. C. Area on which *Nitzschia* would not grow. D. *Chlorella*.

percent of that obtained in previous experiments when *Chlorella* was added initially with *Nitzschia* to new culture medium. The division rate of *Chlorella* added to the *Nitzschia* cultures was thus less than the division rate of *Chlorella* in the control cultures. The decreased division rate and subsequent smaller population obtained in this experiment can be attributed to *Nitzschia* having grown for 2 days in the medium before the addition of *Chlorella*. This gave sufficient time for the medium to become conditioned through the formation and accumulation of the antagonistic substance. The population size and division rate of *Nitzschia* in the cultures to which *Chlorella* was added were not significantly different from those obtained in the control cultures.

INHIBITORY EFFECT ON *NITZSCHIA* OF *CHLORELLA*-CONDITIONED MEDIUM

In the previous experiments when populations of *Chlorella* and *Nitzschia* were grown in mixed cultures, an inhibition always occurred in the growth rate of *Chlorella*, while there was no significant change in the growth rate of *Nitzschia*. Therefore, the following experiment was designed to ascertain whether an inhibition of *Nitzschia* would occur if the medium were conditioned by a longer and larger growth of *Chlorella*. The same procedure used to prepare the *Nitzschia*-conditioned medium was used to prepare the *Chlorella*-conditioned medium, except that *Chlorella* cultures were started with an initial concentration of 70 million cells per liter. At the end of the third day *Nitzschia* was added in sufficient quantity to give 10 million cells per liter to 3 of the *Chlorella* cultures, and 3 *Chlorella* cultures were left as controls. Three flasks with a concentration of 10 million *Nitzschia* cells per liter were prepared as controls.

The size of the *Nitzschia* population reached at the end of the experiment in the mixed cultures was only 70 percent of that attained in the controls (fig. 13). The division rate of the *Nitzschia* cells added to the *Chlorella* cultures were not as great as the division rate of *Nitzschia* in the control cultures. The population size and division rate of *Chlorella* in cultures to which *Nitzschia* was added were not significantly different from those obtained in the control cultures.

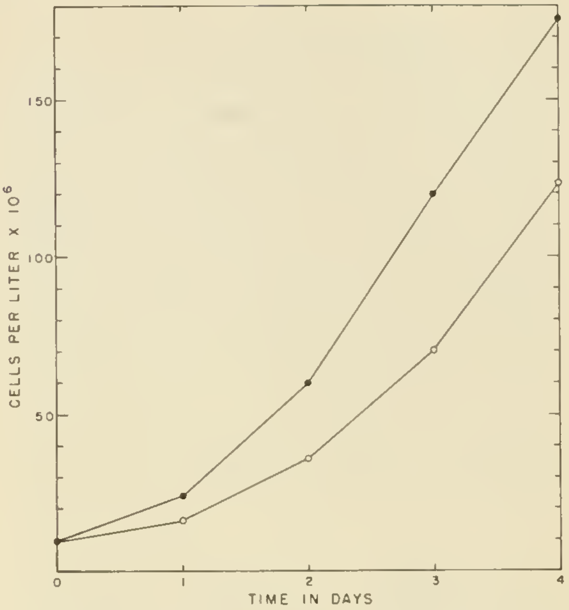

FIGURE 13.—Comparison of growth curves of *Nitzschia* in control and in *Chlorella*-conditioned cultures. Dots represent growth curve in control cultures; circles, growth curve in *Chlorella*-conditioned cultures.

INHIBITORY EFFECTS OF FILTRATE FROM CONDITIONED MEDIA

This experiment was designed to test the growth rates of both *Chlorella* and *Nitzschia* in culture media prepared from the filtrates of their own conditioned media as well as from filtrates of the conditioned medium of the other. *Nitzschia*-conditioned medium was prepared from 5-day-old cultures which had been started with an initial concentration of 10 million cells per liter in standard culture medium. At the end of the fifth day the cultures were centrifuged to remove the cells. The pH was adjusted to 7.0 with phosphoric acid. Phosphate determinations run at this point showed that approximately 5 μgAP/L had been added in the phosphoric acid. Next, 600 cc. of this conditioned medium was filtered through a Berkefeld filter. From this filtered medium, 100-cc. portions were transferred to each of three 250-cc. Erlenmeyer flasks. The remaining 300 cc. of the filtered, conditioned medium was washed with 1-percent Norit A (carbon) by bringing the medium to a boil. The medium was then paper filtered to remove the Norit A, divided into 100-cc. portions, placed in 250-cc. Erlenmeyer flasks, and autoclaved. The same concentration of nutrients used in the standard culture medium was added to both the Berkefeld-filtered medium which had been Norit washed and the medium which was only Berkefeld filtered. Determinations of pH at this point showed that both the Norit-washed, Berkefeld-filtered and the Berkefeld-filtered media had a pH of 7.2±0.1. This was the pH concentration of culture media used in previous experiments. *Chlorella* cultures with an initial concentration of 70 million cells per liter were prepared with both the Berkefeld-filtered and Norit-washed media. Daily cell counts were made for each culture for a period of 7 days. More *Nitzschia*-conditioned medium was prepared but this time both the Norit-washed, Berkefeld-filtered and the Berkefeld-filtered, *Nitzschia*-conditioned media were used for the preparation of *Nitzschia* cultures with an initial concentration of 10 million cells per liter. These cultures were placed on the illuminated shelves and daily cell counts were made for all cultures for a period of 5 days.

Chlorella-conditioned medium was prepared in a way similar to that described for *Nitzschia* except that the *Chlorella* cultures were started with a concentration of 70 million cells per liter, and were grown for 7 days. Culture medium prepared with this *Chlorella*-conditioned medium was used for the preparation of *Nitzschia* cultures with a concentration of 10 million cells per liter, and cell counts were made daily for 5 days. More *Chlorella*-conditioned medium was prepared in the same way, and to the culture medium prepared with this conditioned medium, *Chlorella* cells were added in sufficient quantity to give a concentration of 70 million cells per liter. These cultures were placed on the illuminated shelves and counted each day for 7 days.

As previously stated, standard culture medium was used in the preparation of both *Nitzschia*-conditioned and *Chlorella*-conditioned media. Also, the same amounts of nutrients were again added to the conditioned culture media to be used in further growth studies. Thus, *Chlorella* and *Nitzschia* cells growing in *Chlorella*-conditioned and in *Nitzschia*-conditioned media were being supplied with concentrations of nutrients ranging between 1 and 2 times the concentration used in the standard culture medium. However, in experiments in which *Chlorella* and *Nitzschia* were grown in concentrations of nutrients 1 to 2 times the concentration contained in the standard culture medium, there was no significant difference in the total size of the population or in the division rate. Further experiments showed that the growth of neither *Chlorella* nor *Nitzschia* was changed significantly if distilled water which had been washed with Norit A by bringing the water to a boil was used in the preparation of culture media with the same concentration of nutrients. Therefore no substance which would change the division rate was added to the conditioned medium by washing it in Norit A.

The size of the *Chlorella* populations reached at the end of the seventh day in Berkefeld-filtered and Norit-washed *Nitzschia*- and *Chlorella*-conditioned medium was not significantly different from that obtained in cultures prepared with distilled water and the same concentration of nutrients. The *Chlorella* grown in culture medium prepared from *Nitzschia*- and *Chlorella*-conditioned medium at the end of 7 days had not reached population sizes as large as *Chlorella* grown in similar medium which in addition had been washed in Norit A and autoclaved (fig. 14). *Chlorella* grown in *Chlorella*-conditioned medium reached a population size larger than when grown in culture medium prepared from *Nitzschia*-conditioned medium. Pratt and Fong (1940) have shown in somewhat similar manner that the growth of *Chlorella* is inhibited when grown in culture medium prepared from *Chlorella*-conditioned medium

The division rate of *Chlorella* was not as high in culture medium prepared from Berkefeld-filtered *Nitzschia*- and *Chlorella*-conditioned medium as in the same type of medium which in addition had been washed in Norit A. The division rate of *Chlorella* in Norit-washed *Nitzschia*- and *Chlorella*-conditioned medium was not significantly different from growth obtained in standard culture medium. It can thus be concluded that either the heating of the medium or the washing with Norit A destroyed or absorbed the antagonistic substances formed by these algae. The division rate of *Chlorella* in culture medium prepared from *Nitzschia*-conditioned Berkefeld-filtered medium, which was not washed in Norit A, is less than that obtained in culture medium prepared from *Chlorella*-conditioned, Berkefeld-filtered medium and not washed in Norit A for

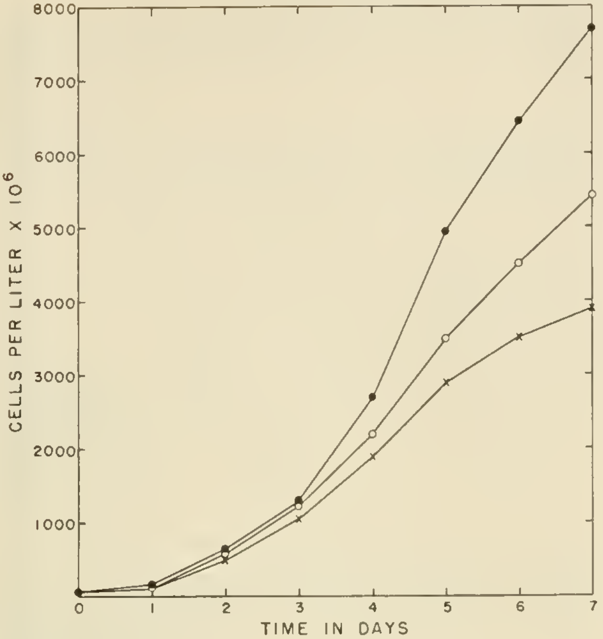

FIGURE 14.—Comparison of typical growth curves of *Chlorella* in culture medium prepared with Norit-washed and autoclaved *Chlorella*- and *Nitzschia*-conditioned medium with *Chlorella*-conditioned medium and with *Nitzschia*-conditioned medium. Dots represent growth curve in culture medium prepared with Norit-washed and autoclaved *Chlorella*- and *Nitzschia*-conditioned medium; circles, growth curve in culture medium prepared with *Chlorella*-conditioned medium; X's, growth curve in culture medium prepared with *Nitzschia*-conditioned medium.

the periods and the numbers of cells used in these experiments.

The size of the *Nitzschia* population reached at the end of the fifth day in Berkefeld-filtered and Norit-washed medium prepared from *Chlorella*- and *Nitzschia*-conditioned medium is not significantly different from that obtained in culture medium prepared with distilled water and the same concentration of nutrients. The *Nitzschia* grown in culture medium prepared from *Nitzschia*- and *Chlorella*-conditioned medium did not reach a population size as large as when grown in similar medium which in addition had been washed in Norit A (fig. 15). *Nitzschia* grown in culture medium prepared from *Nitzschia*-conditioned medium reached a population size larger than when grown in *Chlorella*-conditioned medium. The division rates of *Nitzschia* and of *Chlorella* in culture medium prepared from Berkefeld-filtered, *Nitzschia*- and *Chlorella*-conditioned medium is less than in similar medium which had been washed with Norit A. Thus it has been shown that both *Nitzschia* and *Chlorella* produce substances that remain in the medium after the cells have been filtered off which inhibit not only their own growth but also the growth of the other. Also, the antagonistic substances under the conditions in which they were tested inhibit the growth of the other species more than the species producing them. Finally, it has been determined that these substances can be removed from the medium by filtering and/or washing with Norit A and autoclaving. Lefevre et al. (1949) found that algastatic substances secreted into the medium by one species of alga which caused other species of alga to divide at slower rates could be destroyed by heat.

INHIBITORY EFFECT ON *CHLORELLA* AND *NITZSCHIA* OF *PANDORINA*-CONDITIONED POND WATER

During the time the experiments with conditioned media were being conducted in the laboratory, fluctuations in the phytoplankton populations of Belmont Hill Pond were being followed. This pond was fertilized during the last week of July 1949 and within a period of 3 days a bloom of *Pandorina* appeared with a population of 73 million cells per liter. After this alga had been growing in the pond for a period of 2 weeks and the population had dropped to 46 million cells per liter, a sample was collected and *Chlorella* and *Nitzschia* cultures were prepared as in the previous experiment testing conditioned medium.

Using *Pandorina*-conditioned pond water the population size reached by *Chlorella* after 7 days' growth in medium which had been Berkefeld filtered only was 81 percent of that obtained in similar medium which had also been washed with Norit A and autoclaved (table 1). Similarly, *Nitzschia*, after 5 days' growth in Berkefeld-filtered pond water, reached a population size only 70 percent of that obtained in culture medium which had also been washed with Norit A and autoclaved (table 1). From these observations it can be seen that a substance was present in the pond water which inhibited the growth of both *Chlorella* and *Nitzschia*. Also Lefevre et al. (1949) have grown several species of algae in culture medium prepared with filtered medium in which *Pandorina* had previously grown. Of the

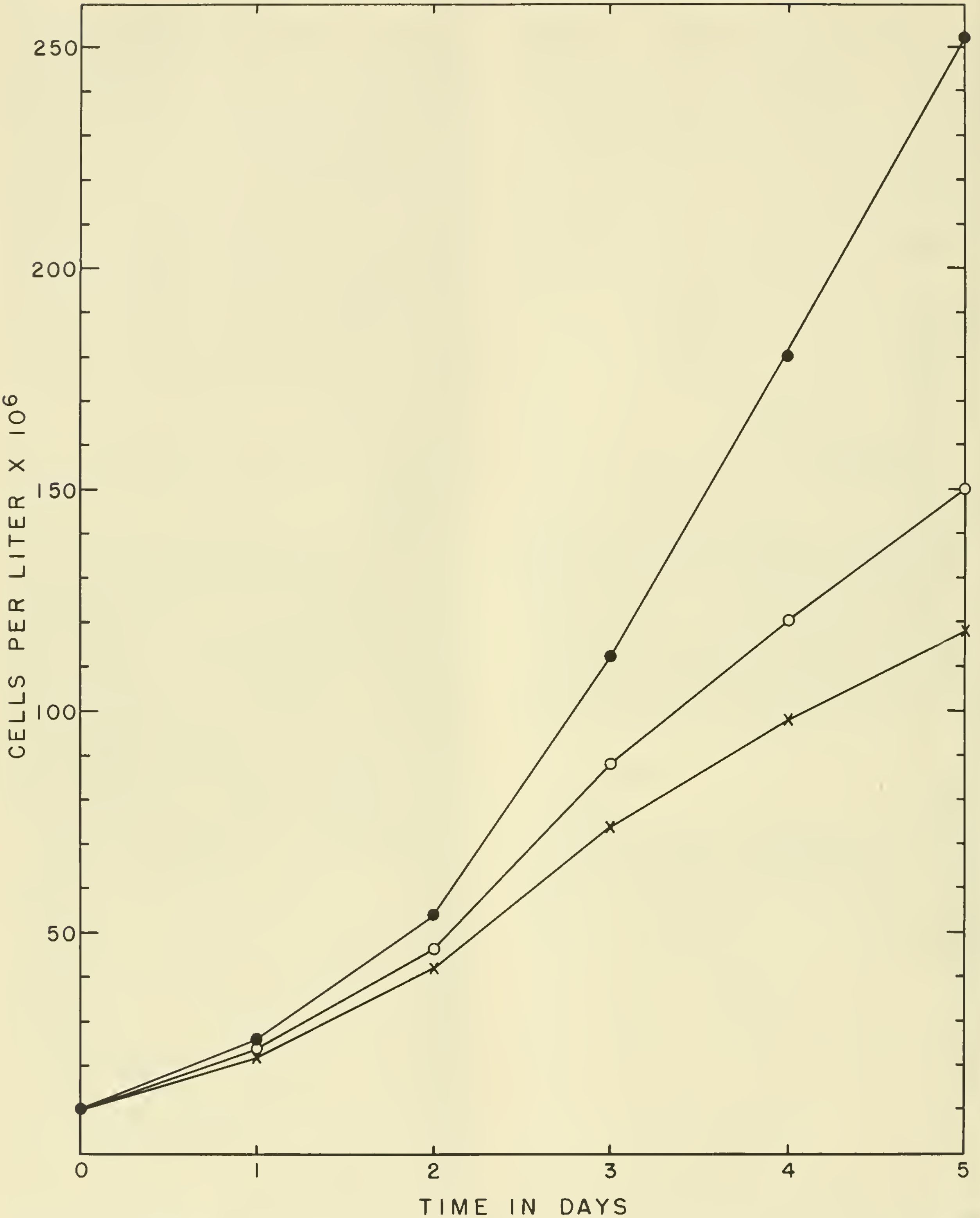

FIGURE 15.—Comparison of typical growth curves of *Nitzschia* in culture medium prepared with Norit-washed and autoclaved *Nitzschia*- and *Chlorella*-conditioned medium, with *Nitzschia*-conditioned medium, and with *Chlorella*-conditioned medium. Dots represent growth curve in culture medium prepared with Norit-washed and autoclaved *Nitzschia*- and *Chlorella*-conditioned medium; circles, growth curve in culture medium prepared with *Nitzschia*-conditioned medium; X's, growth curve in culture medium prepared with *Chlorella*-conditioned medium.

eight species those investigators tested, the majority divided poorly, and some later shrank in size and died.

TABLE 1.—*Populations of* Chlorella *and* Nitzschia *obtained in culture medium prepared from* Pandorina-*conditioned pond water*

[Data given in number of cells per liter]

Culture medium	*Chlorella*		*Nitzschia*	
	Initial population	Population after 7 days	Initial population	Population after 5 days
Pandorina-conditioned pond water:				
Berkefeld filtered	70 x 10^6	6,450 x 10^6	10 x 10^6	195 x 10^6.
Berkefeld-filtered, Norit-washed, and autoclaved.	70 x 10^6	7,930 x 10^6	10 x 10^6	280 x 10^6.
Control:				
Distilled water with standard culture nutrients added.	70 x 10^6	7,690 x 10^6	10 x 10^6	264 x 10^6.

EFFECT OF VARYING THE INITIAL CONCENTRATIONS OF *NITZSCHIA* AND *CHLORELLA*

INHIBITORY EFFECT ON *CHLORELLA* OF INCREASED CONCENTRATIONS OF *NITZSCHIA*

This experiment was designed to test the effect of different concentrations of *Nitzschia* on *Chlorella* populations as listed in table 2. Two cultures were prepared for each population in 50 cc. of standard culture medium buffered with .001 molar K_2HPO_4 and KH_2PO_4 at pH 7.2. The cultures were prepared in 120-cc. Erlenmeyer flasks and cell counts were made for each culture at the end of the first and second days.

Chlorella populations in cultures to which *Nitzschia* was added did not increase as much at the end of the first and second days as the *Chlorella* population in the cultures prepared as controls to which no *Nitzschia* was added (table 2). The larger the initial concentration of *Nitzschia* added to the *Chlorella* cultures the greater the inhibition of growth of *Chlorella*. *Chlorella* populations of 140 million cells per liter to which an initial concentration of 50 million *Nitzschia* cells per liter were added increased approximately threefold in 2 days, while the same size *Chlorella* population to which 150 million *Nitzschia* cells per liter had been added increased only 15 percent in 2 days. *Chlorella* populations of 560 million cells per liter to which an initial concentration of 50 million *Nitzschia* cells per liter were added reached a population size 50 percent of that in the cultures containing only *Chlorella*. Similar *Chlorella* populations to which 150 million *Nitzschia* cells were added were only about 50 percent of populations obtained in *Chlorella* cultures prepared with 50 million *Nitzschia* cells, and 25 percent of those obtained in cultures containing only *Chlorella*. *Chlorella* populations of 1,680 million cells per liter to which 50 million *Nitzschia* cells per liter were added reached 75 percent of the population in the *Chlorella* cultures.

There was no significant difference between the increased size of *Nitzschia* populations when grown in the presence of 140 million *Chlorella* cells per liter and when grown alone (table 2). *Nitzschia* added to *Chlorella* cultures of 560 million cells per liter reached population sizes slightly smaller than those obtained in the control cultures containing only *Nitzschia*, but the difference was not large enough to be significant. The *Nitzschia* added to *Chlorella* cultures of 1,680 mil-

TABLE 2.—*Effect of increased initial concentrations of* Nitzschia *on* Chlorella

[Data given in number of cells per liter]

Type of culture	Initial population of *Chlorella*	Population of *Nitzschia* during first 24 hours	Population of *Chlorella* after 24 hours	Population of *Nitzschia* during second 24 hours	Population of *Chlorella* after 48 hours
Mixed	140 x 10^6	50–140 x 10^6	215 x 10^6	140–245 x 10^6	410 x 10^6.
Do	140 x 10^6	100–250 x 10^6	160x 10^6	250–390 x 10^6	250 x 10^6.
Do	140 x 10^6	150–345 x 10^6	145 x 10^6	345–440 x 10^6	160 x 10^6.
Chlorella [1]	140 x 10^6		325 x 10^6		910 x 10^6.
Nitzschia [1]		50–135 x 10^6		135–260 x 10^6	
Do.[1]		100–280 x 10^6		280–415 x 10^6	
Do.[1]		150–330 x 10^6		330–445 x 10^6	
Mixed	560 x 10^6	50–125 x 10^6	940 x 10^6	125–230 x 10^6	1,310 x 10^6.
Do	560 x 10^6	100–260 x 10^6	825 x 10^6	260–410 x 10^6	910 x 10^6.
Do	560 x 10^6	150–335 x 10^6	680 x 10^6	325–425 x 10^6	745 x 10^6.
Chlorella [1]	560 x 10^6		1,180 x 10^6		3,065 x 10^6.
Mixed	1,680 x 10^6	50–115 x 10^6	2,420 x 10^6	115–195 x 10^6	3,050 x 10^6.
Do	1,680 x 10^6	100–230 x 10^6	2,140 x 10^6	230–360 x 10^6	2,580 x 10^6.
Do	1,680 x 10^6	150–315 x 10^6	1,965 x 10^6	310–405 x 10^6	2,340 x 10^6.
Chlorella [1]	1,680 x 10^6		2,900 x 10^6		4,630 x 10^6.

[1] Control.

lion cells per liter reached smaller populations than those in the control cultures. While this decrease in the *Nitzschia* population was not large enough to be important it occurred in all the mixed cultures. It is believed that the *Chlorella* population was approaching a concentration large enough to bring about an inhibition in the growth of these *Nitzschia* populations. Also the antagonistic substance produced by *Nitzschia* was divided among an increased number of *Chlorella* cells at the beginning of the experiment, thus producing less inhibition.

INHIBITORY EFFECT ON *NITZSCHIA* OF INCREASED CONCENTRATIONS OF *CHLORELLA*

In the previous experiment the effect of varying the initial population of *Nitzschia* on a population of *Chlorella* was tested. Since it has been shown that the concentrations of *Nitzschia* used in the mixed cultures in previous experiments inhibited the growth of *Chlorella*, it was now desirable to test the effect of large concentrations of *Chlorella* on a small concentration of *Nitzschia*. For this experiment, cultures were prepared as in previous experiments, except that different populations of *Chlorella*, as listed in table 3, were used.

The size of the *Nitzschia* population was smaller at the end of the second day in all cultures to which *Chlorella* had been added than in the control cultures containing only *Nitzschia*. The greatest inhibition in the division rate of *Nitzschia* occurred in cultures to which 5,000 million *Chlorella* cells per liter had been added. In these cultures, a 70-percent inhibition occurred in the division rate of *Nitzschia*. In the cultures which contained initially 20 million *Nitzschia* cells per liter and 400 million *Chlorella* cells per liter, a greater inhibition occurred in the division rate of *Chlorella* than of *Nitzschia*. However, in the cultures containing initially 20 million *Nitzschia* cells and 1,200 million *Chlorella* cells per liter considerable inhibition occurred in the division rate of both *Nitzschia* and *Chlorella*.

Since neither nutrients nor pH were limiting factors in these experiments, it can be concluded that the division rate of both *Chlorella* and *Nitzschia* are inhibited by varying the initial concentration of one or the other. The division rate of large concentrations of *Chlorella* is inhibited by relatively small concentrations of *Nitzschia*, while extremely large initial concentrations of *Chlorella* are required to inhibit the division rate of *Nitzschia*. It appears that *Chlorella* is more sensitive to the antagonistic substance produced by *Nitzschia* than *Nitzschia* is to chlorellin.

TABLE 3.—*Effect of increased initial concentrations of* Chlorella *on* Nitzschia

[Data given in number of cells per liter]

Type of culture	Initial population of *Nitzschia*	Population of *Chlorella* during first 24 hours	Population of *Nitzschia* after 24 hours	Population of *Chlorella* during second 24 hours	Population of *Nitzschia* after 48 hours
Mixed	20 x 10^6	400–650 x 10^6	50 x 10^6	650–1,490 x 10^6	135 x 10^6.
Do	20 x 10^6	1,200–2,170 x 10^6	47 x 10^6	2,160–4,970 x 10^6	100 x 10^6.
Do	20 x 10^6	5,000–5,940 x 10^6	30 x 10^6	5,940–9,685 x 10^6	45 x 10^6.
Nitzschia [1]	20 x 10^6		55 x 10^6		140 x 10^6.
Chlorella [1]		400–710 x 10^6		710–2,635 x 10^6	
Do.[1]		1,200–2,670 x 10^6		2,670–6,055 x 10^6	
Do.[1]		5,000–6,230 x 10^6		6,230–10,200 x 10^6	

[1] Control.

EFFECT OF ANTAGONISTIC SUBSTANCES ON PHYTOPLANKTON GROWTH

Up to the present time, our best understanding of the influence one plant exerts on another growing in association with it has been based on knowledge of the competition for some factor essential to growth, such as nutrients. Thus a thorough study was required to demonstrate conclusively the more complicated interactions between *Chlorella* and *Nitzschia* and the existence of antagonistic substances produced by them.

In the experiments reported in this paper, those chemical and physical factors which are known to have an effect upon the growth of algae were eliminated as responsible for the observed inhibition of growth by either maintaining a constant and adequate value for them or having them present in excess. Physical factors such as light and temperature were kept constant within small ranges. Nutrients were added in excess initially to the culture medium in some experiments, and daily to cultures in other experiments. Extreme fluctuation in the hydrogen-ion concentration was prevented by using buffered and aerated medium. The experiment with aerated medium also eliminated lack of CO_2 as a factor responsible for inhibition of growth.

As a precautionary measure to guard against the physiological condition of the cells varying from one experiment to another, controls were run with every experiment. A comparison of the controls in different experiments revealed no significant difference in the physiological condition of the cells used. The control and the mixed cultures were always started with cells taken from the same culture.

The physical effect of one species upon the other in mixed culture cannot be considered as a factor in this inhibition, since experiments with culture medium prepared with conditioned medium from which all cells had been removed gave an inhibitory effect on the growth of cells subsequently cultured in the medium, even though the supply of nutrients and the pH were optimum.

A criticism raised against similar work on the growth of protozoa was that other organisms were used as a source of food for the animals under investigation and that the presence of the supplementary animals in the medium altered the results (Beers 1933; Johnson 1933). This criticism does not apply to the present investigation, since pure cultures of *Chlorella* and *Nitzschia* were used and the liquid media contained only inorganic nutrients. However, the solid medium used to test the effect of chlorellin on *Nitzschia* contained glucose and peptone in addition to the agar. Thus it can be concluded that the inhibition observed in these experiments was due to a substance originating from the algae. The mode of action of these antagonistic substances seemed to be only a retarding effect on the growth rate without any change in pigmentation of the cells or other observable deleterious effects.

Chlorella and *Nitzschia*, through the antagonistic substances produced by them, inhibited their own growth as well as the growth of the other, but each species inhibited the growth of the other more than its own. Rodhe (1948) working with *Scenedesmus* concluded that similar inhibitory conditions existed in his pure cultures.

The fact that a species of alga can inhibit its own further growth under any condition is of extreme importance. In the present laboratory experiments, population densities obtained in pure cultures were much higher than those ordinarily found in nature. Thus a shorter period of time was presumably required for the inhibition to show its effect and the degree of severity probably far exceeds that found under natural conditions. Therefore the results can be applied to natural situations only with caution.

The antagonistic substance produced by *Nitzschia* inhibited the growth rate of *Chlorella* in all experiments in which a concentration of 70 million *Chlorella* cells and 10 million *Nitzschia* cells per liter were used as initial populations. That the antagonistic substance accumulates in the medium of pure cultures as the cultures age was shown. *Nitzschia* cultures with 10 million cells per liter to which *Chlorella* was added on the second day gave a greater inhibition of growth rate for the *Chlorella* cells than when they were added initially with the *Nitzschia*. *Chlorella* cultures started with 70 million cells per liter inhibited the growth of *Nitzschia* when added in a concentration of 10 million cells per liter on the third day. Also when *Chlorella* was grown on agar, the antagonistic substance was absorbed by the agar creating an area on which the *Nitzschia* cells would not grow. An increase in the initial concentration of *Nitzschia* brought about a greater inhibition of the growth rate of *Chlorella*, and a similar increase in the inhibition of small populations of *Nitzschia* was brought about by increasing the initial concentration of *Chlorella*. However, a ratio of *Chlorella* to *Nitzschia* of 20 : 1 was required before the antagonistic substance from *Chlorella* would inhibit the growth rate of *Nitzschia*. When *Chlorella* and *Nitzschia* were grown together with a ratio of 7 : 1, the growth rate of *Chlorella* was always inhibited.

It is possible for antagonistic substances to accumulate in natural bodies of water supporting relatively small phytoplankton populations provided decomposition of these substances is slow. It will be important in the future to determine how long the substances remain effective. Similarly, large populations of phytoplankton may not suppress subsequent growth of certain species if antagonistic substances produced by them are rapidly decomposed. Unfortunately, we have no information as yet on these important points.

In the experiment run with pond water which had supported a large growth of *Pandorina* for 2 weeks preceding the experiment, the growth rate of *Chlorella* was inhibited 19 percent and *Nitzschia* 30 percent in Berkefeld-filtered pond water when compared with growth rates in pond water, which in addition was washed with Norit A and autoclaved.

In natural bodies of water, one species of alga seldom if ever exists completely alone, but blooms are generally dominated by one species. However, during the blooms studied in the pond in these experiments, *Pandorina* became so dominant it is believed that the observed influence of the pond water on the growth rate of *Chlorella* and *Nitzschia* can be attributed to antagonistic substances produced by that dominant species. Another difficulty in the study of the effect of water from ponds, lakes, and the ocean on the growth of phytoplankton is that the water contains, in addition to the inorganic nutrients, organic materials derived not only from the phytoplankton but also from the soil, from animals, and from other plants.

From information obtained in this study and by other investigators, the author suggests that substances originating from phytoplankton may have one of the following effects upon the growth rate of some species of phytoplankton: (1) They may be necessary for any growth, (2) they may stimulate growth, or (3) they may inhibit growth. If these assumptions are correct, it can be seen that the seasonal fluctuations in total phytoplankton numbers and in the numbers of each species, as well as a definite succession of species, may in part be dependent upon the phytoplankton itself.

SUMMARY

1. The growth rates of both *Chlorella* and *Nitzschia* were less when the species were grown together in mixed cultures than when they were grown in pure culture, depending upon the size of the populations used.

2. It was demonstrated that an increase in the inhibition of growth rate of *Chlorella* populations of the same size occurred with an increase in the initial concentration of *Nitzschia*. Similarly, an increase in inhibition of the growth rate of small populations of *Nitzschia* was brought about by increasing the initial concentration of *Chlorella*.

3. If culture medium in which either *Chlorella* or *Nitzschia* had been growing was Berkefeld filtered to remove the cells and nutrients added to the medium and the pH adjusted, the growth rates of both *Chlorella* and *Nitzschia* were inhibited when the species were again grown in this medium. A portion of the same conditioned medium which in addition was washed with Norit A and autoclaved did not inhibit the growth rates of either *Chlorella* or *Nitzschia*. It was thus concluded that the antagonistic substance was either removed or destroyed by the latter treatment.

4. When *Chlorella* was grown on agar the antagonistic substance produced by it was absorbed by the agar and created an area on which the *Nitzschia* cells would not grow.

5. The growth rates of both *Chlorella* and *Nitzschia* were inhibited in culture medium prepared with pond water which had supported a large growth of *Pandorina* for a period of 2 weeks.

6. It is concluded that antagonistic substances arising from the metabolism of phytoplankton are important, at least in fresh-water ponds, in influencing the seasonal fluctuations in total phytoplankton numbers and in the numbers of each species, as well as in causing a definite succession of species.

7. It was found that by transferring a small piece of agar on which *Nitzschia* was growing to the fresh agar, as much growth resulted in 1 week as was previously obtained in from 4 to 6 weeks with transfers made by the conventional bacteriological streaking method.

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CAUSES OF FLUCTUATIONS IN ABUNDANCE OF CONNECTICUT RIVER SHAD

By Reynold A. Fredin

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CAUSES OF FLUCTUATIONS IN ABUNDANCE OF CONNECTICUT RIVER SHAD

By **Reynold A. Fredin**, *Fishery Research Biologist*

This study of fluctuations in abundance of the Atlantic shad (*Alosa sapidissima*) in the Connecticut River is part of a 6-year, coastwise study of the species sponsored by the Atlantic States Marine Fisheries Commission. The United States Fish and Wildlife Service, with the cooperation of the various State agencies along the Atlantic coast, has undertaken to determine the factors affecting the abundance of shad and to recommend measures for restoring the species to its former abundance.

The present commercial shad fishery on the Connecticut River is below Enfield Dam, in Connecticut, 60 miles from the mouth of the river, which rises in Quebec, Canada, and flows southward nearly 400 miles into Long Island Sound, at Saybrook, Conn. An angler's fishery is at the dam. Shad ascend the river as far as Holyoke, Mass., about 85 miles from its mouth, where a dam prevents further upstream movement. What effect the fishway now being constructed at the Holyoke Dam will have on future shad runs is not known.

Nearly all of the shad fishermen on the Connecticut River are gainfully employed in other occupations, but take leave from their jobs each spring during the shad season. After the legal season opens, a few fishermen start fishing at the mouth of the river to determine when the shad enter the river. Shortly after the first shad are taken, other fishermen at the mouth of the river begin operations and are in turn followed by those farther up the river. Fishing continues until the run dwindles. Since the fishermen take time off from their jobs for the sole purpose of fishing, and since the season is short, lasting from 6 to 8 weeks, the fishing effort remains fairly uniform throughout a given season. Logbooks, maintained by a few fishermen for a period of several years, show that once a fisherman commences fishing in a given season he fishes consistently until he stops for the year. Drift gill nets and haul seines are the types of commercial gear used throughout the fishery, except for one pound net located at the mouth of the river at the time of this study.

This paper presents information on some of the factors affecting the abundance of shad in the Connecticut River, such as water temperature, stream flow, pollution, and escapements, and on the basis of catch and effort data for a period of 17 years attempts to relate the fluctuations in abundance of the species to these factors.

Since accurate catch and effort records are prerequisite to determining fluctuations in abundance of shad or of any other species of fish taken commercially, and since a scientific interpretation of these fluctuations should precede any fishery-management recommendations, special recognition is due the Connecticut State Board of Fisheries and Game for having obtained statistics on the Connecticut River shad fishery for a number of years. I wish to thank Dr. R. P. Hunter, Lyle Thorpe, Douglas D. Moss, and other members of the Connecticut State Board of Fisheries and Game, for permission to use shad-fishery statistics and scale data from their official files; for assistance in conducting the field work; and for helpful suggestions pertinent to the investigation.

An expression of appreciation is due to members of the staff of the United States Fishery Laboratory, Beaufort, N. C., who helped in the field work and offered suggestions throughout this study; to Dr. D. B. DeLury, Ontario Research Foundation; Dr. R. J. Monroe, North Carolina State College; Dr. M. B. Schaefer, Inter-American Tropical Tuna Commission; and Elizabeth Vaughn for reviewing this paper; and to the shad fishermen of the Connecticut River without whose cooperation during tagging studies and in turning over their records for review, this work could not have been completed.

STATISTICS OF THE FISHERY, 1890–1951

Although commercial fishermen on the Connecticut River have reported their annual catches of shad to the State of Connecticut since 1890, and the number of licenses issued for shad fishing has been recorded for each year from 1903 to 1930 and from 1932 to 1951 (table 1), this information is not sufficient to determine fluctuations in the abundance of shad over the past 50 years. License data are not a measure of actual fishing effort, since a record of a license issued for a unit of gear does not indicate what proportion of the season the gear was fished. In addition, many of the licensees used small scoop nets and set gill nets which are less than 100 feet long and anchored at one end to the river bank. These two types of gear are used only by part-time fishermen and are comparatively inefficient methods of taking shad.

TABLE 1.—*Shad catch and license data, Connecticut River, 1890–1951*

[Based on table prepared by Douglas D. Moss, Connecticut State Board of Fisheries and Game]

Year	Number of shad caught	Number of nets licensed	Lawful fishing days per week	Year	Number of shad caught	Number of nets licensed	Lawful fishing days per week
1890	34, 318	---------	---------	1921	21, 191	242	---------
1891	22, 462	---------	---------	1922	13, 821	118	7
1892	18, 965	---------	---------	1923	13, 350	163	4
1893	41, 253	---------	---------	1924	25, 316	90	4
1894	72, 398	---------	---------	1925	43, 365	92	5
1895	63, 597	---------	---------	1926	37, 177	96	5
1896	57, 318	---------	---------	1927	34, 321	94	5
1897	73, 367	---------	---------	1928	56, 191	80	5
1898	93, 450	---------	---------	1929	91, 597	99	5
1899	94, 615	---------	---------	1930	66, 136	87	5
1900	114, 182	---------	---------	1931	18, 506	---------	5
1901	124, 927	---------	---------	1932	22, 137	77	5
1902	107, 208	---------	---------	1933	50, 841	61	5
1903	176, 085	130	---------	1934	115, 361	52	5
1904	172, 436	186	---------	1935	128, 106	86	6
1905	120, 358	203	---------	1936	109, 752	81	6
1906	72, 394	176	---------	1937	118, 810	93	6
1907	38, 880	156	---------	1938	127, 283	102	6
1908	49, 031	180	---------	1939	113, 992	67	6
1909	34, 972	150	---------	1940	95, 703	57	6
1910	28, 042	176	---------	1941	125, 160	54	6
1911	27, 640	134	---------	1942	110, 520	54	6
1912	60, 064	106	---------	1943	161, 313	88	7
1913	52, 053	112	---------	1944	214, 086	99	7
1914	58, 075	108	---------	1945	222, 337	116	7
1915	41, 377	155	---------	1946	301, 556	199	6
1916	52, 696	146	---------	1947	223, 358	183	6
1917	64, 766	170	---------	1948	175, 250	167	5
1918	68, 916	195	---------	1949	132, 365	151	5
1919	82, 303	156	---------	1950	77, 090	135	5
1920	50, 312	132	---------	1951	100, 967	121	5

The Connecticut State Board of Fisheries and Game has in its files the annual reports submitted by individual fishermen for 1938 and for the years 1942 to 1951 which give the following information: Total number of shad caught during the fishing season, type of fishing gear used, number of days fished, and location fished. Although the individual reports are not available for the years 1939, 1940, and 1941, records of the total catches made by all fishermen and the number of commercial units (i. e., drift gill nets, seines, and pound nets) used in those years were obtained from the official files. Thus, for a period of 14 years, fishermen's reports provided catch and effort data for the Connecticut River shad fishery.

Fishing is not permitted every day during the time shad are in the river. Prior to each season, the Connecticut State Board of Fisheries and Game sets a number of rest days each week. The number of lawful fishing days a week for the years 1922 to 1951 is shown in table 1.

In totaling the catches reported by the individual fishermen, it was found that set gill nets and scoop nets combined took no more than 3 percent of the total catch in 1938 or in any season between 1942 and 1951. In this paper only the catches made by commercial types of fishing gear are used in the analyses.

A few words concerning the individual reports are in order. When a fisherman used two or more units of the same type of commercial gear, or two or more units of different types of commercial gear during a season, he did not report the catch made by each unit; but rather he gave a single figure for the catch by all units fished. No attempt has been made to differentiate the catches with respect to gear in such cases. From observations of the fishery and discussions with every fisherman on the river during the 1951 season, we learned that a fisherman who obtains licenses for two or more units of commercial gear hires crews of men to assist with the fishing. Once fishing operations begin in any season, it is economical to utilize the crews to the fullest extent, and all available licensed gear is used. Haul seines are generally fished by day and drift gill nets at night. Whenever a fisherman used two or more units of gear during a season and reported that he fished a certain number of days, I have assumed for purposes of this paper that he fished each unit of gear the number of days reported, unless otherwise stated in his report.

CATCH AND EFFORT DATA, 1938 AND 1942–51

Table 2, based on the annual reports of the fishermen filed with the State of Connecticut, shows the number of units of each type of gear in operation, the total number of days fished by each type of gear separately or in combination with other gear, and the total catch by each type of gear separately or in combination, for the years 1938 and 1942–51.

Table 2.—*Catch and effort data, by gear, for the Connecticut River shad fishery, 1938 and 1942–51*

Year	Drift gill net			Haul seine			Pound net			Drift gill net and haul seine combined					Drift gill net and pound net combined				
										Number of units		Net days fished		Number of shad taken	Number of units		Net days fished		Number of shad taken
	Number of units	Net days fished	Number of shad taken	Number of units	Net days fished	Number of shad taken	Number of units	Net days fished	Number of shad taken	Drift gill net	Haul seine	Drift gill net	Haul seine		Drift gill net	Pound net	Drift gill net	Pound net	
1938	28	1,095	63,134	12	405	46,866	1	45	1,856	1	1	45	45	13,500	------	------	------	------	------
1942	20	668	68,645	5	117	14,752	1	55	6,820	4	3	168	127	24,604	------	------	------	------	------
1943	28	1,196	111,178	6	170	13,989	1	60	7,700	2	2	115	115	26,489	------	------	------	------	------
1944	42	1,729	144,248	4	97	11,781	2	97	15,681	5	3	278	166	40,253	------	------	------	------	------
1945	57	2,518	147,448	4	69	4,000	2	125	10.875	8	5	488	303	54,563	------	------	------	------	------
1946	82	3,134	182,188	10	266	21,252	2	81	8,340	17	10	776	456	83,247	1	1	60	60	4,759
1947	80	2,595	110,079	15	461	38,797	1	31	440	20	11	870	478	64,049	1	1	60	60	5,625
1948	74	1,942	71,994	15	390	42,308	1	25	1,240	17	12	659	466	58,290	1	1	50	50	3,400
1949	61	1,715	48,510	21	510	44,725	1	15	304	15	10	499	333	32,974	1	1	48	47	4,082
1950	57	1,473	36,445	22	400	25,359	1	20	300	9	6	251	167	13,146	1	1	40	40	1,840
1951	55	1,438	56,448	16	362	32,734	------	------	------	9	6	276	185	11,785	------	------	------	------	------
Average catch per net day fished	------	------	56.8	------	------	92.5	------	------	74.4	------	------	------	------	------	------	------	------	------	------
Relative efficiency of gear types to drift gill nets	------	------	1.0	------	------	1.6	------	------	1.3	------	------	------	------	------	------	------	------	------	------

When the catch per net-day fished is determined for each type of gear fished separately for each year shown in table 2, and the averages for the 11 years are obtained from the catch-per-net-day-fished values, it can be seen that haul seines took an average of 1.6 times as many fish per day's fishing as drift gill nets, and pound nets took an average of 1.3 times as many fish per day's fishing as drift gill nets. For the population of fish subject to capture by the types of gear used in the fishery, haul seines and pound nets are, respectively, 60 and 30 percent more efficient than gill nets. An adjustment is necessary before the catch per fishing-day effort can be determined, because the effort of a drift gill net fished 1 day is not comparable to that of a haul seine or a pound net fished 1 day. In this study a drift gill net is defined as a standard fishing unit. The fishing power of a standard fishing unit (s. f. u.) is the ability to capture in 1 day a certain fraction of the fish present in the Connecticut River; for a standard fishing unit (a drift gill net), the relative fishing power is taken as unity. The fishing power of the average haul seine is 1.6 times that of the average drift gill net, and it is therefore equal to 1.6 standard fishing units. A pound net is equivalent to 1.3 standard fishing units. The unit of effort is defined as a drift gill net which fishes one day; this will be termed a standard-fishing-unit day. Therefore, a haul seine which operates one day is equivalent to 1.6 standard fishing unit days, and a pound net which operates one day is equivalent to 1.3 standard-fishing-unit days.

The total number of standard-fishing-unit days a season is a measure of the total fishing effort expended and is given for 1938 and for the period 1942 to 1951 in table 3. The numbers of days fished by haul seines and pound nets have been converted to standard-fishing-unit days by using the conversion factors, 1.6 and 1.3.

Table 3.—*Fishing effort, by gear, in standard-fishing-unit days, 1938 and 1942–51*

Year	Drift gill net	Haul seine [1]	Pound net [2]	Drift gill and seine combination		Drift gill and pound combination		Total number of s. f. u. days
				Drift gill	Haul seine [1]	Drift gill	Pound net [2]	
1938	1,095	648	58	45	72	--------	--------	1,918
1942	668	187	72	168	203	--------	--------	1,298
1943	1,196	272	78	115	184	--------	--------	1,845
1944	1,729	155	126	278	266	--------	--------	2,554
1945	2,518	110	162	488	485	--------	--------	3,763
1946	3,134	426	105	776	730	60	78	5,309
1947	2,595	738	40	870	765	60	78	5,146
1948	1,942	624	32	659	746	50	65	4,118
1949	1,715	816	20	499	533	48	61	3,692
1950	1,473	640	26	251	267	40	52	2,749
1951	1,438	579	--------	276	296	--------	--------	2,589

[1] Based on conversion factor, 1.6.
[2] Based on conversion factor, 1.3.

DETERMINING FISHING EFFORT FOR 1935–37 AND 1939–41

Table 3 does not include data for the years 1939, 1940, and 1941, since the original reports were not available, but the number of gill nets, haul seines, and pound nets in operation in those years, obtained from the official files of the State of Connecticut, was as follows:

Year	Gill net	Seine	Pound net	Total
1939	28	11	1	40
1940	20	10	1	31
1941	22	8	1	31

Although it is not known how many days were fished each year, the fishing effort for these 3 years can be estimated in the following way. First, the number of units of gear are converted into standard fishing units.

1939..............28+11 (1.6)+1 (1.3)=47 s. f. u.
1940..............20+10 (1.6)+1 (1.3)=37 s. f. u.
1941..............22+ 8 (1.6)+1 (1.3)=36 s. f. u.

The total fishing effort in a season is measured by the total number of standard-fishing-unit days. From table 3 the total standard-fishing-unit days for 1938 and 1942 are seen to be 1,918 and 1,298, respectively. The number of each type of gear in operation (listed in table 2), in these 2 years is as follows:

Year	Gill net	Seine	Pound net	Total
1938	29	13	1	43
1942	24	8	1	33

When these gear are converted into standard fishing units, the following is obtained:

1938......... 29+13 (1.6)+1 (1.3)=51 s. f. u.
1942......... 24+8 (1.6)+1 (1.3)=38 s. f. u.

The average number of days fished per standard fishing unit in 1938 and 1942 is equal to 1,918/51=37.6 and 1,298/38=34.2, respectively.

An examination of the daily records kept by a few fishermen who have fished since 1930 reveals that these fishermen fished fewer days in 1940 and 1941 than in 1938 and 1939; hence the average number of days fished per standard fishing unit in 1942 was used to estimate the total effort for 1940 and 1941. The average number of days fished per standard fishing unit in 1938 was used to estimate the effort for 1939. The estimated fishing effort in terms of standard-fishing-unit days for 1939, 1940, and 1941 is—

1939......... 47 (37.6)=1,767 s. f. u. days
1940......... 37 (34.2)=1,265 s. f. u. days
1941......... 36 (34.2)=1,231 s. f. u. days

In 1938, 43 of the 102 nets registered were for commercial types of gear that were actually fished; 59 of the licenses were for scoop or set gill nets. The latter type of gear was permitted on the river for the first time in 1935, and in 1938 a total of 22 was in operation. Records are not available for the number of set gill nets licensed in each of the years 1935, 1936, or 1937, for which years 86, 81, and 93 nets were registered (table 1). Douglas D. Moss, aquatic biologist with the Connecticut State Board of Fisheries and Game, has estimated that approximately 25 scoop nets were licensed in each of the 3 years. Scoop nets were popular at that time as they provided many people with the opportunity to catch a few shad for a small outlay of money. The best estimate of the number of nets of commercial type that were actually fished in 1935, 1936, and 1937 appears to be 42 percent of the total number of nets registered in those years, or 36, 34, and 39 units, respectively.

Of the estimated number of units of gear in use in 1935, 1936, and 1937, the best estimate of the proportions of gill nets, haul seines, and pound nets is the proportion of each type that was fished in 1938. The estimated number of each type is as follows:

Year	Gill net	Seine	Pound net	Total
1935	24	11	1	36
1936	23	10	1	34
1937	26	12	1	39

Converting these figures into standard fishing units for each year, we obtain 43, 40, and 46. The 1938 value for the average number of days fished per standard fishing unit is used to estimate the total standard-fishing-unit days for 1935, 1936, and 1937, because the few fishermen who have fished consistently each year since 1930, and from whom records of daily catch and effort are available, fished approximately the same number of days in 1935, 1936, and 1937 as they fished in 1938. Estimates of the fishing effort, or total standard-fishing-unit days for 1935, 1936, and 1937 are 43 (37.6)=1,617; 40 (37.6)=1,504; and 46 (37.6)=1,730, respectively. No attempt is made to determine the fishing effort before 1935, because Mr. Moss has no estimate of the number of scoop nets that were licensed prior to that year.

FISHING EFFORT AND CATCH, 1935–51

The total fishing effort in terms of standard-fishing-unit days has been determined for each year for the period from 1935 to 1951, inclusive. The total catch for each of these years was obtained from reports submitted by the fishermen. For 1938 and the years 1942 to 1951, the reports on file in the office of the Connecticut State Board of Fisheries and Game supplied a record of the catches made by the commercial types of gear. For the years from 1935 to 1937 and 1939 to 1941, for which the individual reports were not on file, but for which records of total catches are available at the State Board of Fisheries and Game, an adjustment for the proportion of catch taken by noncommercial types of gear was made by subtracting 3 percent of the catch from the amount given in table 1. As pointed out earlier, in no one year for which all the individual reports are available was more than 3 percent of the total catch made by noncommercial types of gear. From 1935 to 1937 and from 1939 to 1941, the numbers of noncommercial types of gear operated were no greater than in the other years.

Table 4 shows the total catch, total fishing effort, and catch per unit of effort for each year from 1935 through 1951. The figures entered in this table represent the catch and effort data for the Connecticut River shad fishery for this period. I should like to remind the reader that the figures for fishing effort for 1935, 1936, and 1937 are estimates made from the information available. Figure 1 shows the curves for catch, fishing effort, and catch per unit of effort for the 17-year period.

Table 4.—*Total fishing effort and catch, and catch per unit of effort, Connecticut River shad fishery, 1935–51*

Year	Number of standard-fishing-unit days	Number of shad taken	Number of shad taken per s. f. u. day
1935	1, 617	124, 263	77
1936	1, 504	106, 459	71
1937	1, 730	115, 246	67
1938	1, 918	125, 356	65
1939	1, 767	110, 572	63
1940	1, 265	92, 832	73
1941	1, 231	121, 405	99
1942	1, 298	114, 821	88
1943	1, 845	159, 356	86
1944	2, 554	211, 963	83
1945	3, 764	216, 886	58
1946	5, 309	299, 786	56
1947	5, 146	218, 990	43
1948	4, 118	177, 232	43
1940	3, 692	130, 595	35
1950	2, 749	77, 090	28
1951	2, 589	100, 967	39

ESTIMATING THE SIZE OF THE BASE-YEAR SHAD RUN

Total catch and total effort have been determined for each year from 1935 to 1951. To estimate the population of shad in each of the 17 years, an estimate of total population for a base year was needed. During the 1951 shad fishing season, a tagging program was conducted to determine total population, escapement, and fishing rate. Tagging operations began at the mouth of the Connecticut River shortly after the first shad were taken by commercial fishermen there and were continued through most of the season. Two types of sampling gear were used for tagging. The first was a pound net located near the mouth of the river, the second an anchor gill net used in the mouth of the river. The mesh sizes of the tagging gear covered the range of mesh sizes of the nets used by the commercial fishermen. All fish taken in the gill net were tagged, and a high, nearly uniform proportion of the daily pound-net catch was tagged.

Petersen disk tags, three-eighths inch in diameter were inserted high on the backs of the fish, about one-fourth inch behind the anterior insertion of the dorsal fin. The possibility that the tags made the fish more susceptible to capture was considered. It was hypothesized that if the tags caused selectivity, a higher proportion of tagged fish would occur in the catch at the lower end of the fishery, where the shad were first susceptible to capture, than at the locations farther upstream. It developed that the proportion of tagged fish in the catches in the lower reaches of the river was no greater than in those made farther upstream. That tagging did not increase the fish's susceptibility to capture may be due to the fact that the shad is a deep-bodied fish and, in the Connecticut River, is generally gilled about the head or gills well forward of the point of insertion of the tag.

Biologists contacted each commercial fisherman once a week to pick up recovered tags and pay the 50-cent reward for each tag returned. A few tags were returned by mail. Of 633 Petersen disk tags used, 349 were recovered in the commercial fishery. In addition to the 349 tags actually returned by the fishermen, 10 tags were reported lost or misplaced. Thus the total number of tags accounted for by the commercial fishermen during the 1951 shad fishing season was 359. The proportion of returns of fish tagged from gill nets

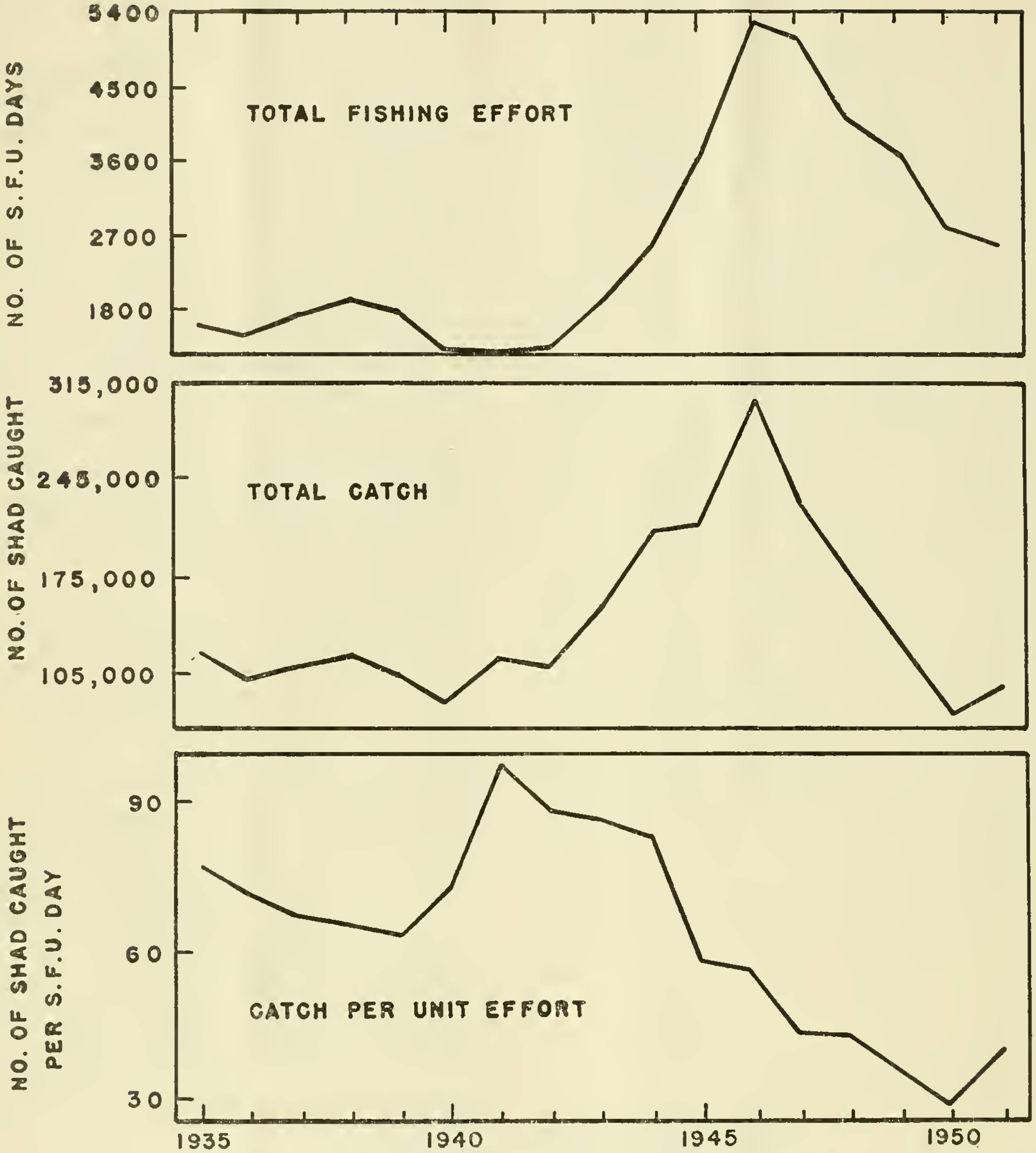

FIGURE 1.—Shad catch, fishing effort, and catch per unit of effort for the Connecticut River, 1935 through 1951

did not differ significantly from the proportion of returns of those tagged from pound nets.

Using the tagging data to estimate the fishing rate, where T equals the number of fish tagged, and T_c the number of tagged fish recaptured, the estimated fishing rate is T_c/T, or 359/633, which equals 56.7 percent. Assuming that the same proportion of untagged fish present in the river was removed by the fishery, where N equals the total population and C equals the catch, the best estimate of N is $\frac{C}{T_c/T}$. The total catch in 1951 was 100,967 shad; therefore, the best estimate of total population would be $\frac{100{,}967}{359/633}$, or $\hat{N}=178{,}072$ fish. Since the estimate of N depends upon T, T_c, and

C, the error in estimating N results from any error in these three quantities.

When C and T are without error, the error in $\hat{N}$ results from the sampling error in T_c; the variance of T_c takes on the form pqn; in this case, it is $(T_c/T)\ (1-T_c/T)\ (T)$, or $T_c(1-T_c/T)$. An approximation to the asymptotic variance of $\hat{N}=\hat{V}(\hat{N})$ is obtained from the expectation of $(d\hat{N})^2$ (Deming 1943) which gives

$$(d\hat{N})^2=\hat{V}(\hat{N})=\frac{T^2C^2(dT_c)^2}{T_c^4} \qquad (1)$$

where $(dT_c)^2$ is equal to $\hat{V}(T_c)$, or $T_c(1-T_c/T)$. For $T=633$, $T_c=359$, and $C=100{,}967$, the estimated variance of $\hat{N}$ is 38×10^6, and the standard deviation of $\hat{N}$ equals 6,175. The reader is referred to papers by Chapman (1948) and Schaefer (1951) for discussions of other formulae for estimating the variance of $\hat{N}$.

DETERMINING SIZES OF RUNS AND ESCAPEMENTS, 1935–50

The fishing power of a standard fishing unit has been defined as the ability of one unit of gear to capture a certain fraction of the fish present in 1 day's fishing. For the Connecticut River shad fishery this fraction will be designated by p and can be considered to be constant within a season and between seasons, provided: (1) There is no innovation in design or manipulation of gear to make it more, or less, efficient as a means of taking fish, (2) the fishing effort is uniform throughout the season, and (3) the migration pattern of shad in the river is similar each year. Daily catch and effort records kept since 1930 by a few fishermen and interviews with many fishermen indicate that the Connecticut River shad fishery meets these three requirements. Table 5 gives the number of days fished each week by a few fishermen who kept records of their fishing activities in past years. The sample is small but it does give an indication that the men fish consistently throughout a given season.

TABLE 5.—*Number of days fished each week during fishing seasons, 1935–51, by sample of Connecticut River fishermen*

Year and fisherman	Number of days fished in week No.—								
	1	2	3	4	5	6	7	8	9
1935:									
Fisherman A	6	6	6	6	6	6	6	6	-----
Fisherman B	6	6	6	6	6	6	6	-----	-----
Fisherman C	6	6	6	6	6	6	6	6	-----
1936:									
Fisherman A	6	5	6	6	6	-----	-----	-----	-----
Fisherman B	6	6	6	6	6	6	6	6	-----
Fisherman C	5	6	6	6	6	6	6	6	-----
1937:									
Fisherman A	1	6	6	6	6	6	6	6	2
Fisherman B	6	6	6	6	6	6	6	6	-----
Fisherman C	5	6	6	6	6	6	6	6	-----
1938:									
Fisherman A	4	6	6	6	6	6	6	5	1
Fisherman B	6	6	6	6	6	6	6	6	-----
Fisherman C	4	6	6	6	6	6	6	6	4
1939:									
Fisherman A	3	6	6	6	6	6	6	5	4
Fisherman B	2	6	6	6	6	6	6	6	-----
Fisherman C	2	2	6	6	6	6	6	6	4
1940:									
Fisherman A	1	2	6	6	6	6	6	6	6
Fisherman B	1	2	6	6	6	6	6	6	-----
Fisherman C	1	2	6	5	6	6	6	6	3
1941:									
Fisherman A	6	6	6	6	6	-----	-----	-----	-----
Fisherman B	2	6	6	6	6	6	6	-----	-----
Fisherman C	6	6	6	6	6	6	5	6	6
1942:									
Fisherman A	6	6	6	6	6	6	6	6	5
Fisherman B	1	6	6	6	6	6	6	6	-----
Fisherman C	6	6	6	6	6	6	6	6	4
1943:									
Fisherman A	4	7	7	7	7	7	7	5	5
Fisherman B	1	7	7	7	7	7	7	7	-----
Fisherman C	5	6	5	6	7	7	7	6	6
1944:									
Fisherman A	3	7	7	6	7	7	5	-----	-----
Fisherman C	3	7	6	6	7	7	7	6	3
Fisherman D	3	4	7	7	7	7	7	7	-----
1945:									
Fisherman A	3	5	4	6	5	5	3	6	7
Fisherman C	5	4	6	5	7	6	5	6	7
Fisherman D	7	7	7	7	7	7	7	7	7
Fisherman E	7	7	7	7	7	7	7	7	-----
1946:									
Fisherman A	3	6	6	6	6	6	6	6	6
Fisherman C	5	6	6	6	6	6	6	5	5
Fisherman E	6	6	6	6	6	6	6	6	6
1947: Fisherman A	5	6	6	6	4	5	-----	-----	-----
1948: Fisherman A	5	5	5	5	5	5	1	-----	-----
1949: Fisherman A	1	5	5	5	5	5	-----	-----	-----
1950: Fisherman A	5	5	5	5	4	-----	-----	-----	-----
1951:									
Fisherman A	3	5	5	5	5	5	5	2	-----
Fisherman D	3	5	5	5	5	5	4	4	-----

Considering the shad run as a whole and denoting its size by N, the number of fish removed in the first standard-fishing-unit day is pN. The number remaining after the first standard-fishing-unit day is qN, where $q=1-p$. The fish that escape in the first standard-fishing-unit day are susceptible to capture in the second standard-fishing-unit day; the number removed during the second standard-fishing-unit day is pqN. The number remaining after the second standard-fishing-unit day, and the numbers removed and remaining after succeeding standard-fishing-unit days are as follows:

	Number removed	*Number remaining*
1st s. f. u. day	pN	qN
2d s. f. u. day	pqN	q^2N
3d s. f. u. day	pq^2N	q^3N
4th s. f. u. day	pq^3N	q^4N
.	.	.
.	.	.
.	.	.
$n-1$ s. f. u. day	$pq^{n-2}N$	$q^{n-1}N$
nth s. f. u. day	$pq^{n-1}N$	q^nN

R. J. H. Beverton (unpublished manuscript) used the model shown above to estimate population parameters for the North Sea demersal fisheries. I have used this model to develop formulae for back-calculating estimates of fishing rates and total populations for an anadromous fishery.

After the nth standard-fishing-unit day, there remain q^nN fish. These fish represent the escapement. The problem is to determine q, then p, since $p=1-q$. From the 1951 tagging data, we have estimates of total population, N, and escapement, E. Table 4 shows that 2,589 standard-fishing-unit days of effort were expended in 1951. Proceeding,

$$\begin{gathered} q^nN=E \\ q^{2589}(178{,}072)=77{,}105 \\ q^{2589}=0.433 \end{gathered} \tag{2}$$

and $q=0.999675$; $p=1-q=0.000325$. In one standard-fishing-unit day 0.0325 percent of the fish remaining are removed. In 1951, for example, where the population is treated as a whole, i. e., $\hat{N}=178{,}072$ shad, in the first standard-fishing-unit day, 58 fish are removed and 178,014 remain; in the second standard-fishing-unit day, 58 fish are removed and 177,956 remain; in the 2,589th standard-fishing-unit day, 25 fish are removed and 77,105 remain.

Given that T_c/T is the fishing rate, then $(1-T_c/T)$ is the escapement rate. It can be seen that $q^n=(T-T_c)/T$. In this case, the sampling error in estimating q results from the sampling error in T_c. An approximation to the variance of q is obtained from the expectation of $(dq)^2$ (Deming 1943). This gives

$$dq=\frac{q(dT_c)}{n(T-T_c)} \tag{3}$$

$$(dq)^2=\hat{V}(q)=\frac{q^2(dT_c)^2}{n^2(T-T_c)^2}.$$

Since

$$(dT_c)^2=\hat{V}(T_c)=T_c(1-T_c/T),$$

$$\hat{V}(q)=\frac{q^2T_c}{n^2T(T-T_c)}$$

For $q=0.999675$, $T_c=359$, $T=633$, $n=2{,}589$, $\hat{V}(q)=3.08\times10^{-10}$, and the standard deviation of q equals 1.75×10^{-5}, or 0.0000175.

To determine the total catch, it is necessary to add the numbers of shad removed in each standard-fishing-unit day, as follows:

$$\begin{aligned} C&=pN+pqN+pq^2N+pq^3N+\ldots+pq^{n-1}N \\ &=pN(1+q+q^2+q^3+\ldots+q^{n-1}) \end{aligned} \tag{4}$$

The expression in the parentheses is the sum of the first n terms of a geometric progression where the first term takes on the value 1 and the common ratio is q. The sum can be expressed by the formula, $\frac{(1-q^n)}{(1-q)}$.

Then,

$$C=pN\frac{(1-q^n)}{(1-q)}, \tag{5}$$

and

$$N=\frac{C}{p\,\frac{(1-q^n)}{(1-q)}}. \tag{6}$$

For any previous year, where the total catch and the number of standard-fishing-unit days are known, we can determine the total population of shad in the river. For example, in 1950 when the total catch was 77,090 shad and total effort 2,749 standard-fishing-unit days, the total population is estimated as follows:

$$\begin{aligned} \hat{N}&=\frac{77{,}090}{0.000325\left[\frac{1-0.999675^{2749}}{1-0.999675}\right]} \\ &=\left[\frac{77{,}090}{0.588}\right]=131{,}105 \end{aligned} \tag{7}$$

The annual fishing rate for 1950 is estimated to be 58.8 percent, and the total escapement is 54,015 shad.

Formula 6 has been used to estimate the total population, annual fishing rate, and escapement for each year that catch and effort data are available. These estimates are given in table 6 for the period from 1935 to 1951.

Some workers may question the validity of treating the river run of an anadromous species as a whole, since all the fish do not enter the river simultaneously. However, if the 1951 run were treated as a number of groups entering the river throughout the season and the number of fish in each group were known, it would be possible to determine p provided catch figures for each group were available and fishing effort were uniform for each group. With uniform fishing effort, p would remain constant throughout the season. Further, this p value could be used to determine total populations and escapements for other years where we have (1) the same number of groups

TABLE 6.—*Estimated total population, annual fishing rate, and escapement of shad in the Connecticut River shad fishery, 1935–51*

Year	Number of s. f. u. days	Number of shad taken	Annual fishing rate	Total population ($\hat{N}$)	Escapement ($\hat{E}$)
			Percent		
1935	1,617	124,263	40.6	306,066	181,803
1936	1,504	106,459	38.4	277,237	170,778
1937	1,730	115,246	42.7	269,897	154,651
1938	1,918	125,356	46.1	271,922	146,566
1939	1,767	110,572	43.4	254,774	144,202
1940	1,265	92,832	33.5	277,110	184,278
1941	1,231	121,405	32.8	370,137	248,732
1942	1,298	114,821	34.2	335,734	220,913
1943	1,845	159,356	44.8	355,705	196,349
1944	2,554	211,963	56.1	377,831	165,868
1945	3,764	216,886	70.3	308,515	91,629
1946	5,309	299,786	81.9	366,039	66,253
1947	5,146	218,990	81.0	270,358	51,368
1948	4,118	177,232	73.5	241,132	63,900
1949	3,692	130,595	69.6	187,636	57,041
1950	2,749	77,090	58.8	131,105	54,015
1951	2,589	100,967	56.7	178,072	77,105

entering the river, (2) uniform fishing effort throughout the season, and (3) catch statistics by groups.

Although the runs may vary from year to year with regard to the length of time they last, the number of groups in the runs can be assumed to be uniform each year. Certain river conditions may speed up or retard the passage of the entire run through the fishery, but such a situation is the sum of the effects of the river conditions on the individual groups. A large run may take longer to pass through the fishery, but in this case the individual groups can be considered to be larger in size and require a longer period of time to move up the river. Because of the nature of the Connecticut River shad fishery, the fishing effort can be considered to be uniform throughout a given season. Catch records cannot show the catch by groups because of mixing of groups within the river; therefore, the number of fish in each group cannot be determined. For this reason, I have treated the runs as a unit. The results obtained by treating the runs either as a whole or in parts are identical. The same estimates of total population and escapement prevail.

FACTORS AFFECTING THE SIZE OF CONNECTICUT RIVER SHAD RUNS, 1940–51

FISHING

The total population of shad in any year includes fish which are susceptible to capture for the first time and fish which, although they were susceptible to capture the previous season, have managed to escape the fishery and return to the river to spawn again. The expressions, "catchable recruits" and "repeaters," will be applied to these two groups of fish.

The ages of nearly 2,000 fish taken in the 1951 commercial catch were determined by a scale-reading technique developed by J. P. Cating (1953). Of the catchable recruits, 90 percent were 4- or 5-year-old fish that were spawning for the first time. The remaining 10 percent were shad returning to the river for the first time as 3-, 6-, and 7-year-old fish and a few 4-year-old males that had spawned once, but, as will be pointed out later, were too small to be caught by the commercial gear the first time they spawned.

The three major components of the total population are 4-year-old catchable recruits, 5-year-old catchable recruits, and repeaters. The relationships among total population in year i, escapement or brood stock size in year $i-5$, escapement or brood stock size in year $i-4$, and escapement in year $i-1$, can be evaluated by means of multiple regression. Further, the amount of information furnished in advance by the escapement data can be determined. The following data are incorporated in table 7: Total population for each year from 1940 to 1951 with the corresponding escapements 1, 4, and 5 years earlier; predicted total populations, $\hat{Y}$; the deviations from regression, $Y-\hat{Y}$; the regression equation; the partial correlation coefficients; an analysis of variance for multiple regression; and the multiple correlation coefficient.

The R value obtained is significant at the 1-percent level; it can be inferred that 83 percent of the variation in total population can be accounted for by changes in the escapements from the fishery. Of the three partial correlation coefficients shown in table 7, $^{r}YX_3 \cdot X_1X_2$ is highly significant, and $^{r}YX_1 \cdot X_2X_3$ approaches significance; on the other hand $^{r}YX_2 \cdot X_1X_3$, although positive, is small. The low value of $^{r}YX_2 \cdot X_1X_3$ may be explained by the possibility that the 4-year-old catchable recruits did not contribute as greatly to the runs in years prior to 1951 as they did in 1951 when the major components of the runs were determined from commercial scale samples. Further scale collections from the commercial catch will yield more information on this.

TABLE 7.—*Multiple regression of estimated population in year i (Y) on escapement in year $i-5$ (X_1), escapement in year $i-4$ (X_2), and escapement in year $i-1$ (X_3), with population expected from regression ($\hat{Y}$) and deviation from expected population ($Y-\hat{Y}$), in thousands of fish*

Year (i)	X_1 E_{i-5}	X_2 E_{i-4}	X_3 E_{i-1}	Y $\hat{N}_i$	$\hat{Y}$	$Y-\hat{Y}$
1940	182	171	144	277	310	−33
1941	171	155	184	370	331	39
1942	155	147	249	336	371	−35
1943	147	144	221	356	343	13
1944	144	184	196	378	335	43
1945	184	249	166	309	353	−44
1946	249	221	92	366	320	46
1947	221	196	66	270	277	−7
1948	196	166	51	241	243	−2
1949	166	92	64	188	214	−26
1950	92	66	57	131	162	−31
1951	66	51	54	178	141	37

$$\hat{Y}=48.10655+0.52543X_1+0.31298X_2+0.78338X_3$$

$$r_{YX_1 \cdot X_2X_3}=0.413,\ P\sim0.25$$

$$r_{YX_2 \cdot X_1X_3}=0.253,\ P\sim0.48$$

$$r_{YX_3 \cdot X_1X_2}=0.818,\ P<0.01$$

ANALYSIS OF VARIANCE

Source:	*Degrees of freedom*	*Sum of squares*	*Mean square*
Total	12	1,040,752	------
Mean	1	963,333	------
Regression	3	64,490	21,497
Error	8	12,929	1,616

$$F=\frac{21,497}{1,616}=13.303,\ P<0.01$$

$$R^2=0.833;\ R=0.912,\ P<0.01$$

ENVIRONMENTAL CHANGES

The deviations from regression in table 7 reflect the effects of other factors on the total population of shad. Water temperatures, stream flow, and dissolved oxygen data have been carefully studied, but none of these variables exhibits changes or trends that would account for the changes in total population or the deviations from the predicted populations. However, until representative samples of scales are taken from the commercial fishery for a series of years and the year-class sizes are estimated, it is not possible to determine fully the effects of these variables during the spawning season on the size of the year class.

EXTRANEOUS MORTALITY

One factor which may affect the deviations from regression is the mortality which occurs among the adult shad between fishing seasons. This mortality could be from natural causes during or following spawning in the river, natural causes at sea, or from fishing outside the river. The 1951 tagging experiment and similar studies by Hollis (unpublished manuscript), and Westman and Bevelander (correspondence with Dr. Westman), show that Connecticut River shad are taken by fishermen off the coast of Maine, in Sandy Hook, Raritan and Lower New York Bays, off Long Island, and along the New Jersey coast.

The mortality that occurs among the adult shad between fishing seasons will be referred to as extraneous mortality in this paper. If scale samples representative of the commercial catch with respect to gear and sex were available for a number of years, the extraneous mortality rates could be easily estimated. Since most of the scale samples have been collected from the highly selective gill-net fishery in the past, it is necessary to use scale data from the sport fishery at Enfield Dam.

The Connecticut State Board of Fisheries and Game has collected scale samples at the Enfield Dam sport fishery each year since 1944. These samples represent from 10 to 33 percent of the anglers' catches and are taken in the same manner each year. Before these scale samples can be used for mortality determinations, the assumption must be made that the fish caught at Enfield Dam are representative of the fish escaping the commercial fishery. An examination of the lengths and ages of fish taken by anglers at the dam reveals proportionately more small 3-year-old males in the sport-fishery samples than in the commercial-fishery samples. The apparent disproportionate number of small males may be due to the fact that some of these fish are too small to be caught by commercial gear, or may result from a lack of samples from the haul-seine fishery which generally takes more small male shad than does the gill-net fishery. Only when more representative samples from the commercial catch are obtained can the discrepancy be explained. In the meantime, I do not believe one can safely assume that the small males in the sport-fishery samples are representative of the fish escaping the commercial fishery each year.

Even though the relative abundance of all other fish is assumed to be the same in the Enfield Dam samples as in the group of fish escaping the fishery, the effects of disproportionate numbers of 3-year-old males in the Enfield samples can cause serious errors in mortality-rate determinations. For this reason, in estimating mortality rates I have selected 2 successive years when the 3-year-old males were in the same proportionate abundance in the sport-fishery samples.

In 1946, the proportion of 3-year-old males in the sample from Enfield Dam was 21.9 percent; the proportion in 1947 was 22.6 percent. These are the only 2 successive years in which the proportionate abundance of 3-year-old males in the Enfield Dam sample was similar. In 1946, the 6-year-old class predominated in the Enfield Dam samples. The total and extraneous-mortality rates among this group of fish for 1 year will be determined.

Where

P_6 = the proportion of 6-year-old fish in the sample from Enfield Dam in 1946,
P_7 = the proportion of 7-year-old fish in the sample in 1947,
E_{1946} = the estimated total escapement in 1946,
E_{1947} = the estimated total escapement in 1947,

then,

$n_6 = P_6E_{1946}$ = the number of 6-year-old fish that escaped the fishery in 1946.
$n_7 = P_7E_{1947}$ = the number of 7-year-old fish that escaped the fishery in 1947,

and

$\frac{n_6-n_7}{n_6}$ = the total mortality rate among 6-year-old fish for 1 year.

During the course of a year, the 6-year-old shad are subject to mortalities from two sources: extraneous mortality and fishing mortality in the river. Extraneous mortality occurs prior to the following season's fishing mortality in the river; the number of deaths by extraneous causes is assumed to be negligible during the fishing season. Where M_x is the extraneous mortality rate and M_f is the river fishing mortality rate, the total number of deaths among the 1946 6-year-old group is:

$$M_xn_6+M_f(n_6-M_xn_6)=n_6-n_7; \qquad (8)$$

further,

$$M_x=\left[\frac{n_6-n_7}{n_6}-M_f\right]\div(1-M_f)\cdot \qquad (9)$$

The total and extraneous mortality rates of the 6-year-old shad escaping the fishery in 1946 are estimated as follows:

E_{1946}=66,253.
E_{1947}=51,368.
$M_{f,1947}$=0.810.
K_1=the number of fish sampled at Enfield Dam in 1946=1,183.
K_2=the number of fish sampled at Enfield Dam in 1947=1,344.
P_6=proportion of 6-year-old fish among K_1 fish $=\frac{273}{1,183}=0.231$.
P_7=proportion of 7-year-old fish among K_2 fish $=\frac{48}{1,344}=0.036$.
$n_6=P_6E_{1946}=0.231(66,253)=15,304$.
$n_7=P_7E_{1947}=0.036(51,368)=1,849$.
$\frac{n_6-n_7}{n_6}=\frac{15,304-1,849}{15,304}=0.879$=the total mortality rate.

$$M_x=\frac{.879-.810}{1-.810}=0.363.$$

An approximation to the variance of M_x is obtained from the expectation of $(dM_x)^2$ (Deming 1943):

$$(dM_x)^2=\hat{V}(M_x)=\left[\frac{\frac{P_6^2P_7(1-P_7)}{K_2}+\frac{P_7^2P_6(1-P_6)}{K_1}}{P_6^4}\right]\left[\frac{E_{1947}}{E_{1946}(1-M_f)}\right]^2 \qquad (10)$$

For the case presented, $(\hat{V}M_x)=0.009195$; the standard deviation is approximately 0.096.

The number of 6-year-old shad that escaped from the fishery in 1946 and died from extraneous causes before returning to the river in 1947 is estimated to be 0.363 (15,304), or 5,555 fish. The commercial fishery in the river removed 0.81 (15,098–5,345), or 7,897 fish of this age class. Thus, of the total of 13,452 deaths, about 40 percent occurred outside the Connecticut River shad fishery, and the effect of the extraneous mortality on the 6-year-old group of shad was nearly as great as the river-fishing mortality. Extent of fluctuation in the extraneous-mortality rate from year to year is not known, but if a standard sampling technique is followed in the collection of scales from the commercial catch, and samples are taken each year for a number of years, the extraneous-mortality rate can be estimated each year and changes in it determined.

It was pointed out earlier that tagging studies have shown that Connecticut River shad are taken by fishermen off the coast of Maine, in Sandy Hook, Raritan, and Lower New York Bays, off Long Island, and along the New Jersey coast. One of the causes of extraneous mortality could be fishing in these areas.

From the New Jersey Division of Fish and Game and the New York Conservation Department, the records of the catches of shad (in pounds) by pound-net fisheries off the New Jersey coast, in Sandy Hook, Raritan, and Lower New York Bays, and off Long Island have been obtained for the years 1946 to 1950, as follows:

Year	New Jersey coast, Sandy Hook, and Raritan Bay	Lower New York Bay	Long Island	All areas combined
1946	500, 000	176, 000	120, 000	796, 000
1947	303, 000	253, 000	36, 000	592, 000
1948	573, 000	224, 000	48, 000	845, 000
1949	411, 000	95, 000	55, 000	561, 000
1950	480, 000	204, 000	(1)	(2)

[1] Not available.
[2] Incomplete.

The number of pound nets in operation by New Jersey fishermen increased each year from 144 in 1946 to 180 in 1950. Dr. James Westman, Rutgers University, has informed me that before 1945 the Long Island pound nets were usually not put in operation early enough in the spring to fish for shad; but since 1945 the Long Island pound nets have fished for shad. It is interesting that negative deviations from regression occur in 1947, 1948, 1949, and 1950 in table 7. The negative deviations from regression reflect an adverse condition such as an increased extraneous mortality which might be related to an increase in pound-net effort.

The relation between pound-net catches and deviations from the expected populations in the Connecticut River cannot be fully evaluated at this time because the extent to which Connecticut River shad contribute to these pound-net catches is not known. Additional tagging studies conducted in the areas where pound nets are fished would enable us to determine the effect of this fishing on the Connecticut River shad runs. The causes of the extraneous-mortality rate must be taken into consideration in a management program to restore the Connecticut River shad population to the level of abundance which it held in the early 1940's.

CONCLUSIONS AND RECOMMENDATIONS

The Connecticut River shad reached a peak of abundance in the middle 1940's, the runs becoming smaller after 1946. According to analyses of population and escapement data, over 80 percent of the fluctuations in the size of the runs can be attributed to changes in the size of the escapement from the fishery. For a given number of shad entering the river, the proportion of fish escaping the fishery depends upon the fishing rate. The fishing rate not only was higher from 1944 to 1951 than it was from 1935 to 1943 (table 6), but the average size of the runs since 1944 has been smaller. The conclusion is that the decline in the abundance of shad since the middle 1940's can be attributed, chiefly, to overfishing in the river. The extraneous-mortality rate might also affect the size of the run entering the river. If further studies show that the extraneous-mortality rate is a function of ocean pound-net fishing, the problem of restoring the shad runs to their former level of abundance broadens in scope; the pound-net fisheries, as well as the river fishery, would have to be managed. However, one inference from analysis of the data is clear: when the escapement totals are increased, the size of the runs in later years may be expected to increase.

As a result of the studies conducted in the Connecticut River, the following conclusions have been reached relative to the management of the shad fishery: The size of the shad run can be predicted one season in advance within desired limits of confidence, fishing effort and fishing rate can be estimated prior to the beginning of the season; hence the fishing effort should be adjusted to permit escapement of a predetermined number of shad.

Until additional information is obtained on the extraneous-mortality rate, the river-fishing effort should be maintained at a level that will permit adequate spawning escapements to build up the Connecticut River shad run. For the present, the river-fishing effort should not exceed the 2,589 standard-fishing-unit days of effort expended in 1951.

The most important contributions that can be made toward the management of the river fishery are the continued collection of scale samples and the maintenance of catch and effort records from the commercial fishery. The scale samples should be representative of the fish taken with respect to gear and sex. Accurate fishery statistics, that is, catch and effort data, should be collected for the pound-net fisheries along the New Jersey coast, in Sandy Hook and Lower New York Bays, and off Long Island. Tagging studies should be conducted from the pound-net fisheries of New York and New Jersey to determine the proportion and number of Connecticut River shad that are taken by these fisheries.

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FLUCTUATIONS IN THE FISHERIES OF STATE OF MICHIGAN WATERS OF GREEN BAY

BY RALPH HILE, GEORGE F. LUNGER
AND HOWARD J. BUETTNER

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FISHERY BULLETIN 75

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

ABSTRACT

Production records for 1885, 1891–1908, and 1929–49, indicate cyclic fluctuations for several important species of fish. The average annual take (all species) of 3,582,000 pounds in 1929–49 was 3,503,000 pounds below the 1891–1908 mean of 7,085,000 pounds. Decline in the output of lake herring alone from 5,841,000 pounds in 1891–1908 to 1,070,000 pounds in 1929–49—a drop of 4,771,000 pounds—more than accounted for the decrease. For species other than lake herring the combined output increased from 1,244,000 pounds in 1891–1908 to 2,512,000 in 1929–49—a rise of 1,268,000 pounds.

The 1929–49 fluctuations of abundance (as estimated from records of catch per unit of effort) were considerable for all principal species. In the late years of the period, lake trout were scarce as the result of sea-lamprey depredations, but the abundance levels of whitefish, lake herring, and walleyes were extremely high; at the same time the smelt was showing good recovery from the disastrous 1943 mortality. With certain exceptions, correlations between fluctuations of fishing intensity and the abundance of individual species were low, probably because most operations are based on several species and hence not ordinarily sensitive to changes in the abundance of a particular one.

A combination of intensive fishing and high abundance of three principal species carried the production to 5½ million pounds in 1947 and the modern record high of between 7½ and 8 million pounds in 1948 and 1949. With this prosperity has developed a most difficult situation arising from friction between local commercial fishermen and newcomers from other areas and from the activities of sport fishermen and resort owners who believe that drastic restrictions on commercial fishing will insure a perpetual high level of abundance of walleyes.

Statistics for 1950 are given in a supplement.

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